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THESIS – THÈSE

Title of Thesis – Titre de la thèse

Systematics of the Holarctic ground-beetle subgenus Chrysobracteon Netolitzky and related Bembidion Latreille (Coleoptera: Carabidae)

Degree for which thesis was presented Grade pour lequel cette thèse fut présentée Master of Science	Year this degree conferred Année d'obtention de ce grade 1985
University – Université The University of Alberta	Name of Supervisor – Nom du directeur de thèse George E. Ball

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Systematics of the Holarctic ground-beetle subgenus *Chrysobracteon* Netolitzky and related *Bembidion* Latreille (Coleoptera: Carabidae)

by

©

David Robert Maddison

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF Master of Science

Department of Entomology

EDMONTON, ALBERTA
Fall 1985

THE UNIVERSITY OF ALBERTA

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DEGREE FOR WHICH THESIS WAS PRESENTED Master of Science

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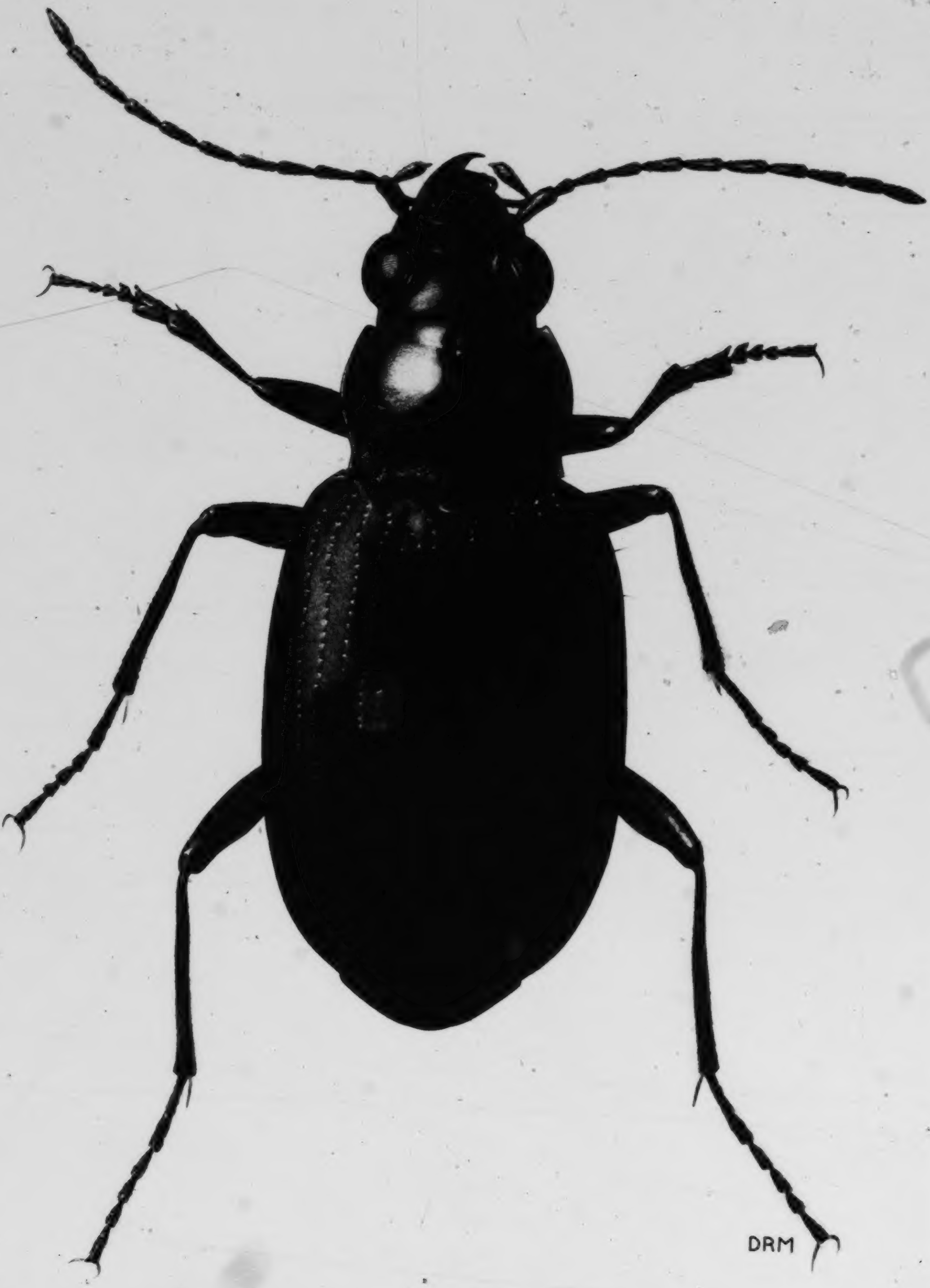

Frontispiece. *Bembidion (Chrysobracteon) alaskense* Lindroth, adult male, Killik River, Alaska. Length about 5.2 mm.

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled **Systematics of the Holarctic ground-beetle subgenus *Chrysobracteon* Netolitzky and related *Bembidion* Latreille (Coleoptera: Carabidae)** submitted by David Robert Maddison in partial fulfilment of the requirements for the degree of Master of Science.

George E Ball

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G. H. Gooding

Richard C. Fox

Date August 22, 1985

ABSTRACT

A review of the classification of the Holarctic subgenus *Chrysobracteon* Netolitzky reveals seventeen valid species (six Palearctic, eight Nearctic, and three Holarctic). The names *B. colvillense* Lindroth and *B. alaskense* Lindroth are newly synonymized. *B. levettei carrianum* Casey is resurrected as a northern and eastern subspecies of *B. levettei* Casey, while the subspecies *B. inaequale opaciceps* Casey is no longer recognized.

On the basis of a detailed study of structure of adults and larvae, *Chrysobracteon* is grouped with the subgenera *Odontium* LeConte (synonyms: *Bracteon* Bedel, *Cylindrobracteon* Netolitzky) and *Ochthedromus* LeConte to form the *Odontium* subgeneric group. *Ochthedromus* and *Odontium* are briefly characterized; within *Ochthedromus*, the name *B. cheyennense* Casey is removed from synonymy with *B. bifossulatum* LeConte.

For adults, keys are provided to subgenera of the *Odontium* subgeneric group, and for species of *Chrysobracteon*. For larvae, a key is provided to known first instars of the *Odontium* subgeneric group.

States of 81 characters of *Chrysobracteon* and nineteen additional species of the *Odontium* subgeneric group, as well as nineteen other *Bembidion* species plus *Asaphidion alaskanum* Wickham, are described. Characters studied are from adult structure, including male and female genitalia, as well as first instar larvae and chromosomes. Some phylogenetic relationships within *Odontium*, *Ochthedromus*, and *Pseudoperyphus* Hatch are inferred using these characters; the traits also serve as evidence for a phylogenetic analysis of *Chrysobracteon* itself.

In a review of species concepts, a species of dioecious organisms is described as a part of a lineage, where a lineage is a cohesive major portion of the genealogical nexus. To fully understand phylogeny, techniques must be used and explored that detect dichotomizing lines as well as anastomosing lines, including the anastomosing between pedigrees of individual organisms.

In a review of principles and methods for reconstructing phylogenies, Maximum Likelihood Estimation of phylogenies and Wagner Analysis are compared. A choice between these numerical techniques, and related non-numerical methods, depends in part upon what assumptions about evolutionary processes are warranted at the outset of phylogenetic analysis. For a poorly-known group such as *Chrysobracteon*, a cautious approach is advised, using a minimum of background assumptions. A mental form of Wagner analysis (a parsimony approach) is used, with minimal weighting: only characters that are subject to observation errors, or are polymorphic within at least two species, are weighted against.

I conclude (tentatively) the following cladistic relationships of *Chrysobracteon* species. *B. balli* Lindroth and *B. foveum* Motschulsky are sister species, and together form the sister group to the rest of *Chrysobracteon*.

B. argenteolum Ahrens, *B. alaskense*, and *B. semenovi* Lindroth form a monophyletic group, whose sister group appears to be *B. stenoderum* Bates. The sister group of that four-species assemblage is the *B. carinula* Chaudoir + *B. velox* (Linné) + *B. lapponicum* Zetterstedt clade; within the latter clade, *B. velox* appears to be more closely related to *B. lapponicum*; the placement of *B. carinula* is tentative. The seven species from *B. argenteolum* to *B. lapponicum* form a monophyletic group whose sister group of seven species all possess the derived chromosome number 2n=20+XY. The 2n=20+XY clade consists of three lineages of uncertain relationships: *B. hesperium* Casey, *B. lorquinii* Chaudoir, and the *B. inaequale*-subgroup. Within the *B. inaequale*-subgroup, *B. zephyrum* Fall is the sister group to the rest. Cladistic structure of the five remaining taxa (*B. levettei levettei*, *B. levettei carrianum*, *B. inaequale* Say, *B. litorale* (Olivier), *B. baikaloussuricum* Netolitzky) of the *B. inaequale*-subgroup remains unresolved, except that *B. litorale* and *B. baikaloussuricum* are hypothesized to be sister species. I am not able to specify the sister group of *B. punctatostriatum* Say.

Widespread dispersal and resulting sympatry of these lowland beetles has clouded past vicariant events, causing difficulty in inferring biogeographic events. A meager discussion of historical geographic movements of lineages is presented; ages and barriers for phylogenetic or biogeographic events are not inferred.

ACKNOWLEDGEMENTS

When I arrived at the University of Alberta in 1981, I had a great deal to learn about beetles, science, and people. While much discovery still lies ahead of me, I have learned and gained many things during my stay. My single most important guide through these all-too-few years has been my supervisor, G.E. Ball. With his wealth of understanding of living creatures, and his care for his work and people, he has served as an inspiration and an invaluable source of advice.

R.C. Fox and my brother, Wayne P. Maddison, have been similarly significant sources of enthusiasm, encouragement, and wisdom, for which I am very grateful. Wayne's help in obtaining copies of literature should not go unmentioned. R.H. Gooding graciously acted as my supervisor during G.E. Ball's administrative leave, as well as fulfilling, along with R.C. Fox and G.E. Ball, the duties of being a member of my supervisory committee. The three members of my committee also thoroughly and competently reviewed the manuscript.

I heartily thank Diane Hollingdale, Kerry P. Irons, and, most especially, Helen M. Amerongen for being precious friends at important times. Helen's aid during the last stages of the study was vital for the maintenance of progress and my sanity; she also helped tremendously with photography. Felix A. H. Sperling and John H. Acorn provided essential companionship throughout much of my stay in

Edmonton.

The members of the Department of Entomology, especially my fellow graduate students, have all helped in numerous ways. I will mention only a few of their contributions.

Many people aided me in various technical endeavours. W.P. Maddison, G.E. Ball, N.E. Stork, F.A.H. Sperling, J.E. O'Hara, K.C. Jope of the United States National Park Service, J.H. Acorn, and K.P. Fennie helped in collecting specimens. D.J. Larson and J. Andersen provided advice for raising larvae. H. Goulet obtained larvae of eastern *B. inaequale* and a few other eastern *Bembidion* for me. T. Nakane sent some valuable specimens of *Chrysobracteon* and related groups from Japan for me. T.L. Erwin and H. Goulet suggested valuable techniques for studying male genitalia. D.A. Craig helped me with matters microscopic and photomicroscopic. G. Braybrook patiently taught me how to use the SEM, and provided other necessary services. F.A.H. Sperling translated some essential papers from German to English; K.P. Fennie provide a translation of Keleinokova (1976). R.E. Roughley borrowed the type and only known specimen of *B. semenovi*, and hand-carried it from Leningrad so that I might study it. A. Sen and B.K. Mitchell aided my study of sensilla by providing advice and bibliographic help. I sincerely thank all of these people.

In my efforts to obtain a working version of the computer program PAUP, David L. Swofford spent a great deal of time and energy, for which I am very grateful.

Allen G. Supynuk and George Carmichael, both of University of Alberta Computing Services, also helped above and beyond the call of duty. I also thank Mike M. Miyamoto for helping to arrange a transfer of the program source files from the University of Michigan computer.

To all of the curators of collections listed in "Specimens Examined", I express my gratitude for their help in obtaining much of the material on which this study is based.

This work was funded primarily by NSERC Grant A-1399 to G.E. Ball.

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1. INTRODUCTION

On bare sand beaches of northern lakes and rivers, small ground beetles, whose intricately microsculptured surfaces reflect silver and gold, scamper in the bright sunlight of warmer days. These beetles are members of the Holarctic subgenus *Chrysobracteon*, an eminently appropriate name for them, as it is derived from the Greek "χρυσξσ", meaning gold, and the Latin "*bractea*", meaning a thin metal plate, or scale.

The first of seventeen known *Chrysobracteon* species to receive a name was *Bembidion velox*, described by Carl von Linné in 1761. Since then, nearly sixty formal names have been applied to members of *Chrysobracteon*. The Palearctic fauna was first comprehensively studied by Netolitzky (1940, 1942, 1943) and Lindroth (1940). Lindroth's later (1962, 1963, 1965) examination of world *Chrysobracteon* included the first review of all known Nearctic species; his work forms the foundation for present worldwide studies of the subgenus.

Netolitzky and Lindroth provided descriptions of external adult structure and male genitalia of the species of *Chrysobracteon* that they recognized. For the most part, I confirm their conclusions on delineation of extant species, and expand their study of character systems to include female genitalia and chromosomes. As well, I extend Andersen's (1966) work on Palearctic *Chrysobracteon* larvae, describing larvae of eleven Nearctic species.

This character analysis served not only to help delimit species, and provide aids for their identification, but also to supply the datum base for the primary purpose of this work: the first study of evolution of members of the subgenus.

A necessary background for such investigations is the placement of *Chrysobracteon* into its phylogenetic context; that is, a deciphering of relationships of the subgenus to other carabids. To set the stage for the *Chrysobracteon* study, therefore, I have had to re-examine the cladistic structure of the near-relatives of *Chrysobracteon*. I present results of this preliminary work, discussing the relationships of some of the species of *Odontium* and *Ochthedromus*, groups closely related to *Chrysobracteon*. I also give a brief review of the relationships of the subgenera of *Bembidion*, the genera of the Bembidiina, and the subtribes and tribes of the supertribe Trechitae. I include a redescription of the genus *Bembidion*, and notes on the subgenera related most closely to *Chrysobracteon*, belonging to the *Odontium* subgeneric group.

Because of the variety of techniques of phylogeny reconstruction presently in use, and the controversies about their use, I discuss at some length principles and methods of reconstructing phylogenies, and reasons behind my choice of methods for *Chrysobracteon*. Similar, but shorter, sections are devoted to the species concept I use and biogeographic methods.

The thrust of my work is on the relationships of species, and present patterns within extant species, such as geographic variation, I treat only superficially. My short discussion of biogeography of the group is thus restricted to historical movements of lineages.

An extensive character analysis serves as the basis for the core of this paper: a detailed examination of the phylogeny of *Chrysobracteon*.

2. MATERIALS AND METHODS

2.1 Specimens studied

About 10,100 adult, 550 first instar, 60 second instar, and 30 third instar larval specimens of Recent *Chrysobracteon* were examined routinely; a smaller sample of specimens was studied in greater detail. I have included sample sizes for most of the data presented. One Pleistocene and 14 Miocene fragments were also available. About 500 Recent adults and 70 larvae of other subgenera of *Bembidion*, and of related genera, were studied as well. Acronyms, addresses, and curators of collections cited in the text, and from most of which specimens were borrowed, are listed below. Acronyms are used throughout the text.

AMNH	Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York, 10024 U.S.A. (L.H. Herman)
AMor	A. & A.V. Morgan, Department of Biology, University of Waterloo, Waterloo, Ontario, N2L 3G1 Canada
BCPM	British Columbia Provincial Museum, Parliament Buildings, Victoria, British Columbia, V8V 1X4 Canada (R.A. Cannings)
BHar	Brian Harrison, #405 - 16 Lakewood Drive, Vancouver, British Columbia, Canada
BJCa	B.F. and J.L. Carr, 24 Dalrymple Green NW, Calgary, Alberta, T3A 1Y2 Canada

BMNH	British Museum (Natural History), Cromwell Road, London SW7 5BD, England (N.E. Stork)
CAS	Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California, 94118 U.S.A. (D.H. Kavanaugh)
CNC	Canadian National Collections of Insects, Arachnids and Nematodes, Biosystematics Research Institute, Research Branch, Ottawa, Ontario, K1A 0C6 Canada (A. Smetana)
CUIC	Cornell University Insect Collections, Department of Entomology, Cornell University, Ithaca, New York, 14853 U.S.A. (Q.D. Wheeler)
DEUN	University of Nebraska State Museum, Research and Systematics Collections, W-436 Nebraska Hall, Lincoln, Nebraska, 68588 U.S.A (B.C. Ratcliffe)
DHKa	David H. Kavanaugh, Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, California, 94118 U.S.A.
DRMa	David R. Maddison, Department of Entomology, University of Alberta, Edmonton, Alberta, T6G 2E3 Canada
FMNH	Field Museum of Natural History, Roosevelt Rd. and Lake Shore Dr., Chicago, Illinois, 60605 U.S.A. (J. Keethley and J.S. Ashe)
GDND	Geology Department, North Dakota State University, Fargo, North Dakota, 58105 U.S.A. (D.P. Schwert)
HNHM	Hungarian Natural History Museum, H-1088 Budapest,

	Baross u.13., Hungary (Z. Kaszab)
ICCM	Carnegie Museum of Natural History, Section of Entomology, 4400 Forbes Avenue, Pittsburgh, Pennsylvania, 15213 U.S.A. (G. Ekis and R. Davidson)
ISAs	I.S. Askevold, Department of Entomology, University of Manitoba, Winnipeg, Manitoba, R3T 2N2 Canada
JHAc	J.H. Acorn, Department of Entomology, University of Alberta, Edmonton, Alberta, T6G 2E3 Canada
JKLi	J.K. Liebherr, Department of Entomology, Cornell University, Ithaca, New York, 14853 U.S.A.
JVMa	J.V. Matthews, Jr., Terrain Sciences Division , Geological Survey of Canada, Ottawa, Ontario, K1A 0E8 Canada
KUSM	Snow Entomological Museum, University of Kansas, Lawrence, Kansas, 66044 U.S.A. (P.D. Ashlock)
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, 02138 U.S.A. (A.F. Newton, Jr.)
MNHP	Entomologie, Muséum National d'Histoire Naturelle, 45 Rue Buffon, Paris Ve, France
OSUC	Department of Entomology, Ohio State University, Columbus, Ohio, 43210 U.S.A. (C.A. Triplehorn)
OSUO	Oregon Systematic Entomology Laboratory, Department of Entomology, Oregon State University, Corvallis, Oregon, 97331 U.S.A. (G.L. Peters)
ROM	Department of Entomology, Royal Ontario Museum, 100 Queens Park, Toronto, Ontario, M5S 2C6 Canada (G.B.

	Wiggins)
SAEl	Scott A. Elias, Instaar Box 450, University of Colorado, Boulder, Colorado, 80809 U.S.A.
SMNH	Saskatchewan Museum of Natural History, Wascana Park, Regina, Saskatchewan, S4P 3V7 Canada (R.R. Hooper)
TBau	Thomas Bauer collection, Univ. Regensburg, Zoologisches Institut, Universitätsstraße 31, D-8400 Regensburg, Federal Republic of Germany
UASM	Department of Entomology, University of Alberta, Edmonton, Alberta, T6G 2E3 Canada (G.E. Ball & D. Shpeley)
UBC	Spencer Entomological Museum, Department of Zoology, University of British Columbia, Vancouver, British Columbia, V6T 2A9 Canada (S.G. Cannings)
UCB	California Insect Survey, Division of Entomology and Parasitology, University of California, Berkeley, California, 94720 U.S.A. (J.K. Liebherr and J.A. Chemsak)
UMHF	Division of Entomology, Zoological Museum, University of Helsinki, N. Järnvägsgatan 13, SF-00100 Helsinki 10, Finland (H. Silfverberg)
UMSP	Department of Entomology, Fisheries, and Wildlife, University of Minnesota, St. Paul, Minnesota, 55101 U.S.A. (P.J. Clausen)
UMMZ	The University of Michigan, Museum of Zoology, Division of Insects, Ann Arbor, Michigan, 48109 U.S.A. (B.M. O'Connor)

USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., 20560 U.S.A. (T.L. Erwin and W.N. Mathis)
UWLW	Entomological Museum, University of Wyoming, Laramie, Wyoming, 83070 U.S.A. (R.J. Lavigne)
ZIL	Zoological Institute, Academy of Sciences of U.S.S.R., 199164, Leningrad, U.S.S.R. (O.L. Kryzhanovskij)
ZMLS	Museum of Zoology and Entomology, Lund University, Helgonavägen 3, S-223 62 Lund, Sweden (R. Danielsson)
ZMUM	Zoological Museum, Moscow University, Moscow, U.S.S.R.

2.2 Collecting *Chrysobracteon*

On cloudy, cool days, *Chrysobracteon* adults were found in cracks and burrows in sandy banks of river, creek, lake, and ocean shores. They were forced onto the surface by flooding the banks with water, and then were collected by hand; larvae were also occasionally captured by this method. On sunny and warm days, however, the beetles were active on the surface and flew if disturbed. They were best stalked with a net in hand. Most adults were killed with ethyl acetate.

Most larvae were obtained using a modification of the techniques of J. Andersen and D.J. Larson (pers. comm. 1981). Adult females and males were kept in clear plastic boxes half-filled with damp, uncontaminated sand, and fed moistened pieces of Purina Puppy Chow® or Safeway Complete and Balanced Cat Food® which were changed daily. Freshly killed insects and spiders were added on occasion. First instar larvae appeared in the sand one to eight weeks later. Some were raised to later instars on the same diet. Larvae were killed in boiling water and stored in Barber's solution or 70% ethanol. All descriptions are based on larvae raised *ex ovo*.

2.3 Specimen preparation and examination

Wild M5® and Leitz Model RS® stereo dissecting microscopes were used to study external structures of dried adults. Permanent microscope slides were made of one or two adults of each species (except *B. semenovi* Lindroth and *B. baikaloussuricum* Netolitzky). These specimens were disarticulated and cleared, using hot 10% KOH to remove soft tissue and warm 1:1 95% ethanol:30% hydrogen peroxide solution to reduce pigmentation, before being mounted in Euparal®. Cleared adults, genitalia, and larvae were examined using a Leitz SM-Lux® brightfield microscope at 100X or 400X. Some structures were examined with a Cambridge Stereoscan 250® Scanning Electron Microscope.

Preparation procedures for study of some characters are described in more detail below.

2.3.1 Genitalia

Most studied genitalia were dissected out of water-softened adults, placed in hot 5-10% KOH (aq.) for ten minutes to remove soft tissue, and then transferred via distilled water and 95% ethanol into the observation medium. Membranous portions of female genitalia were stained with chlorazol black in 70% ethanol. I examined the majority of genitalia in glycerin, except for those illustrated by line drawings, which were mounted in either Euparal® or cedarwood oil.

Some internal sacs of dried males were everted by suction (using a technique suggested by K.W. Cooper and H. Goulet, pers. comm.) after water-softening and hot KOH treatment. The suction device consisted of a syringe with a thin plastic tube in place of a needle. At the end of the plastic tube was a glass capillary tube, drawn so that the internal diameter at its tip was slightly greater than the width of a *Chrysobracteon* aedeagus. By placing this capillary tube over the apex of the aedeagus, but not over the parameres, suction could be applied to the median lobe without the whole genitalia being sucked into the syringe. The internal sac was carefully sucked out in water or weak acetic acid, then transferred to 70% ethanol for storage.

Most everted sacs studied were prepared by a superior technique, requiring live specimens, suggested by T.L. Erwin (pers. comm.). A live adult male was held between fingers under a dissecting scope, and gently squeezed until the genitalia and then the internal sac popped out. While being careful to maintain pressure, I grasped the specimen with a pair of forceps, and held it in boiling water for a few seconds. It was then released, and allowed to cook for about

20 seconds, hard-boiling the contents of the internal sac. The beetle was then placed in 70% ethanol for storage, or through 95% ethanol and amyl acetate in preparation for critical point drying. The female genitalia illustrated in Figs. 185-187 were prepared by the same forced eversion technique.

2.3.2 Larvae

Permanent microscope slides of cleared larvae were made by a technique similar to Goulet's (1977, 1983:226). Specimens were transferred from water through a graded series of KOH solutions into 5% KOH (aq.), which was heated to a gentle boil. After internal tissues cleared, larvae were cooled and taken through a graded series of solutions from 5% KOH down to distilled water then up to 95% ethanol; specimens were transferred with a wide-mouthed eyedropper. Larvae were placed in a weak (about 5%) solution of Euparal® in 95% ethanol, and eventually became impregnated with the mounting medium as the ethanol evaporated. To speed evaporation and prevent unwanted precipitation of Euparal, the weak Euparal solution with larvae was placed in open glass vials on a low-heat hotplate, with an electric fan close by blowing air over the vial tops. After impregnation, the larvae were mounted on slides.

2.3.3 Chromosomes

For most examined species, hypothesized counts and sex-chromosome systems are based on observations of male meiosis as well as male and female mitosis of Feulgen-stained squash preparations. Male and female mitoses were not observed in *B. levettei levettei*, and females of *B. lorquinii* were not studied cytogenetically. For details of the method used, see Maddison (1985).

2.4 Measurements

The following measurements of adults and larvae were made using an eyepiece reticle on a Wild M5 or Leitz SM-Lux:

ADULTS:

Hl	length of head, along midline, from apex of clypeus to posterior margin of left eye;
Pl	length of pronotum along midline;
Pwm	maximum width of pronotum in front of hind angles;
El	length of elytra, from tip of scutellum to apex;
SBL	standardized body length, SBL=Hl+Pl+El;

LARVAE:

LFl	length of frontale of larval head along midline;
LCl	length of coronal suture;
LHl	head length = LFl + LCl;
LHw	width of head behind posterior stemmata.

Standardized body length (SBL) is used as a measurement of overall length that is not subject to the effects of varied membrane folding or body position. Unfortunately, there are two "standardized body length" definitions within carabid literature, because of two definitions of head length or Hl. Ball (1972) defines Hl as "straight-line distance from base of mandible to posterior margin of compound eye, on left side of head", whereas Kavanaugh (1979) treats head length as "length of head, measured along midline from apical margin of clypeus to a point opposite posterior margin of eye". Whitehead (1972), and Erwin and Kavanaugh (1981) use head length measures equivalent to Kavanaugh's. I use Kavanaugh's definition, as it is closer to the "apparent" length of the head from the neck to the apex of normally resting mandibles, and thus SBL is closer to apparent body length.

2.5 Illustrations

All drawings of beetle parts were made with a Wild M5® or Leitz SM-Lux® microscope, using a *camera lucida*, except for the frontispiece, for which photographic slides were used to aid in reproducing proportions. Scanning electron micrographs were produced using a Cambridge Stereoscan 250® Scanning Electron Microscope. Photographs of cleared structures were taken with a Carl Zeiss Ultraphot II®.

2.6 Terms

The diacritical mark (!) indicates I examined the specimens being discussed.

For most structures of adults, I use terms employed by Ball and Shpeley (1983). Nomenclature of elytral setae, genitalia, and larval sensilla posed some special problems, which will now be discussed in turn. A few other terms are defined in the section "Character states in *Chrysobracteon*", or as required in the text.

Erwin and Kavanaugh's (1981) nomenclature of setae of bembidiine elytra is used for the most part. However, within *Chrysobracteon*, there is considerably more variation in number and position of elytral setae than in most bembidiine species, making it difficult to identify homologous setae. For example, in most bembidiines, the umbilical series is constantly segregated into a humeral set of four setae (eo1 to eo4), and a subapical set of four to five setae (eo5 to eo9, Fig. 4). Within *Chrysobracteon*, the umbilical series varies. In most specimens, two setae are present in the position of eo5 and eo6, but they occasionally number one or three. In some species, there are no umbilical setae between eo4 and eo5. In others, additional setae are present (Fig. 4), of various numbers, with as many as five setae between eo4 and eo5 on one elytron (as in the holotype of *B. semenovi*). I do not give these additional setae names (although "eo4.2", "eo4.4", and so on, could be used). I designate as eo4 the fourth most anterior umbilical seta, and eo5 and eo6 as the most posterior two setae in the position of Erwin and Kavanaugh's (1981) eo5 and eo6. The names of pre-eo4 and post-eo5 setae follow from these designations (Fig. 4).

Lindroth (1940) developed a nomenclature for male internal sac structures of several Old World species of *Bembidion*. Among species of a subgenus, Lindroth used the same name to denote homologous features. But between subgenera, no such homology is implied. Thus his "Ch1" for *Chrysobracteon* specimens is undoubtedly not homologous to the "Ch1" of *Philochthus*. Erwin and Kavanaugh (1981) use names taken mostly from Lindroth (1940) for their treatment of the *Bembidion wickhami* (=*B. carlhi*, see Erwin (1984)) and *B. erasum* groups; indeed, the internal sac sclerites they name are probably homologous to homonymous structures shown by Lindroth (1940) for *Philochthus*. From my meager investigation of the male genitalia of *Bembidion*, I cannot determine the nature of homologies between sclerites named by Erwin and Kavanaugh and those seen in *Chrysobracteon*. Because of this, I avoid Lindroth's and Erwin and Kavanaugh's letter and number codes, and use instead descriptive names (Figs. 99-102). These are discussed in more detail later, in the characterization of *Chrysobracteon*.

Names of parts of beetle spermathecae vary from author to author, so that discussion of structure of these organs becomes difficult. I have chosen to follow Howden (1976) and

Gordon (1985) in calling the basal bulb, near the attachment of the spermathecal duct, the nodulus; the area of attachment of the spermathecal gland, the ramus; the portion protruding beyond the ramus, the cornu (Fig. 165).

Notation of most larval sensilla follows that proposed by Bousquet and Goulet (1984). Their admirable system works very well for *Chrysobracteon*; that is, the sensilla of *Chrysobracteon* larvae are for the most part in about the same positions as figured by Bousquet and Goulet (1984). I have encountered two difficulties in using their nomenclature. First, they name only setae and flat, circular sensilla of the exterior surface (their "pores"). Their system does not include hypopharyngeal sensilla, nor most sensilla on the apical articles of the maxillary palp, galea, and labial palp, and apical two antennomeres. While this is a limitation of their system, it is not a criticism of the excellent foundation they provided. The second difficulty is in the division of the names into two groups, one (a two-letter upper-case sclerite or organ code as well as an arabic number) for setae, and the other (a two-letter upper-case sclerite or organ code as well as a lower-case letter) for "pores". This division is based not on study of function, nor detailed electron microscope study of structure, but rather on appearance under a light microscope. Most of the "setae" in their system are probably trichoid sensilla, and most of the "pores" are probably chordotonal organs, but there are exceptions. For example, the "pore" FRf (Figs. 194,204) is most likely a contact chemoreceptor. Bousquet and Goulet's (1984) nomenclature may need to be revised, but for now I will use it; however, I will avoid the word "pore" for any small sensillum.

2.7 Names of taxa

Numerous names given to members of *Chrysobracteon* have primary types deposited in collections in Europe. I have examined none of these (with the exception of the single known specimen of *B. semenovi*), and instead rely on Lindroth's (1962, 1963) interpretation of types and names. As his concepts of the species of *Chrysobracteon* were almost identical to mine (only a few of our placements of specimens differ), I doubt that re-examination of the types he studied is crucial at present.

However, Lindroth (1962, 1963) did not consider some early (pre-1961) names, as he thought they were described as mere aberrations, and did not study types of these names. Some of these were originally described as varieties, and are available names (ICZN Third Edition Article 45(g)). I list all of these names, including those clearly of infrasubspecific rank, and note those I consider unavailable.

As well, primary types of many *Chrysobracteon* names where thought by Lindroth to be lost. These include several Motschulsky names, the types of which have been rediscovered (Keleinikova 1976). These types need to be restudied (I have not yet seen them), to either confirm or refute the present tentative interpretations of the names. Other types have not yet been found. I make no effort to locate these types, nor to designate neotypes. Work in European museums is necessary before this can be accomplished.

Publication dates of most *Chrysobracteon* names are not controversial, except for those described by Netolitzky (1940, 1942). Lindroth (1962, 1963) considered Netolitzky (1940) to constitute a valid publication, and thus treated the names *Litoreobracteon*, *Argyrobracteon*, *etc.*, as being published in 1940; he viewed the 1942 paper as a republication. Erwin and Sims (1984) as well as Netolitzky himself (1942) appear to consider the 1940 paper as unpublished, and state the publication date of those names as 1942. Apparently only reprints of the 1940 paper were issued (Lindroth 1962:18 and Netolitzky 1942:29). If Netolitzky distributed these reprints, then the paper does constitute a valid publication (ICZN Third Edition Article 8). A search of North American libraries by the University of Alberta discovered not one copy; a search by Lund University of major western European libraries came up with similarly negative results (L. Cederholm, pers. comm.). However, the work was publicly distributed, at least to some extent, as a library in Chernovsti, Ukraine possesses a copy (L. Cederholm, pers. comm.), although I do not know at what date they received it. Until more information is gathered (I am now awaiting a copy from Chernovsti)), I cannot judge the status of Netolitzky (1940), and will cite both dates (1940 and 1942) for any nomenclatorial acts published in both papers.

2.8 Systematic procedures

Methods used for inferring species limits are described later, under "Species and subspecies recognition" (p. 75). Techniques used to infer the phylogeny and biogeography of *Chrysobracteon* and its relatives are discussed in the sections about phylogenetic and biogeographic analysis of *Chrysobracteon*. Although the results of phylogeny reconstruction are used as part of the foundation for the supraspecific classification that follows, I defer discussion of the phylogeny reconstruction until the classification is presented and the species are described.

3. CHARACTERIZATION OF SUPRASPECIFIC TAXA

3.1 Genus *Bembidion* Latreille

Bembidion Latreille, 1802:82. [Type species *Carabus quadriguttatus* Fabricius, 1775:248 (=*B. quadrimaculatum* Linné 1761:211), designated by Jeannel (1941:475).] (Generic synonymies given by Erwin and Sims 1984.)

3.1.1 Notes on the type species

The originally included nominal species are *B. biguttatum* (Fabricius) and *B. quadriguttatum* (Fabricius) (Latreille 1802), and thus one of these nominal species must serve as the type species of the genus (ICZN Third Edition, Article 69). Andrewes's (1935) designation of *B. quadrimaculatum* is therefore invalid. As he did not explicitly state that he considered *B. quadriguttatum* Fabricius to be a synonym of *B. quadrimaculatum* Linné (as is now believed (Jeannel 1941, Lindroth 1974a)), his designation does not constitute a fixation of the former as type species (ICZN Third Edition Article 69(a)(v)). Jeannel's (1941) statements do, however, constitute a valid designation, which is ironic considering his preference for *B. biguttatum* as the type (Jeannel (1941:475-476, footnote)). The recognition of *B. quadriguttatum* rather than *B. quadrimaculatum* as the type should not alter existing nomenclature so long as they are considered synonymous or to belong to the same subgenus.

3.1.2 Species included

I follow Netolitzky (1942, 1943), Lindroth (1963, 1976, 1980), and Erwin and Kavanaugh (1981) in treating *Bembidion* as a very large genus with perhaps more than a thousand species, including almost all members of the subtribe Bembidiina. I conservatively follow Erwin (1972) and Lindroth (1963, 1976, 1980) in excluding from *Bembidion* members of *Asaphidion* Gosiz, *Phrypeus* Casey, *Bembidarenas* Erwin, and *Zecillenus* Lindroth; all other Bembidiina are included within the genus.

In contrast, Jeannel (1941) split *Bembidion* into numerous genera (17 in the French fauna alone), and several European systematists have followed suit (for example, Jeanne 1971, and other titles in the same series; Antoine 1955). Perrault (1981) has recently adopted an intermediate position; he splits *Bembidion* into ten genera world-wide. Unfortunately, rigorous phylogenetic studies of the lineages within bembidiines have yet to be performed, and as a result the cladistic structure of the subtribe Bembidiina as a whole is unclear. If future world-wide studies reveal distinct major lineages, it may prove best to divide *Bembidion* into a few smaller genera, as Erwin (1974) has done for tachyines. However, until *Bembidion* is better known, I think it best to retain the broad generic concept and avoid fragmentation into poorly resolved groups.

Papers dealing extensively with systematics of *Bembidion* on a local or global scale include Andrewes (1935), Antoine (1955), Basilewsky (1968, 1972), Casey (1918, 1924), Darlington (1959, 1962), Erwin (1982, 1984), Erwin and Kavanaugh (1981), Hayward (1897, 1901), Jeannel (1941, 1962), Jedlička (1961, 1965a), Kryzhanovskij (1983), Larochelle (1977), Lindroth (1940, 1945, 1954, 1955, 1962, 1963, 1965, 1974a, 1976, 1980), Müller (1918, 1926-1927), Netolitzky (1914a, 1927, 1940, 1942, 1943), Pawlowski (1974), Perrault (1981, 1982), and Schuler (1959).

Evidence for the monophyly (or lack thereof) of *Bembidion* is discussed under "The Phylogenetic Context of *Chrysobracteon*"; here I give only a characterization of members of the genus. This is difficult, if not impossible, to do well at present, in part because of the large number of species in the taxon, but also because of the lack of knowledge of most members of *Bembidion*. I have gleaned information in the following diagnoses and description from Andrewes (1935), Netolitzky (1942, 1943), Lindroth (1940, 1963, 1976, 1980), Erwin (1982), Erwin and Kavanaugh (1981), Erwin and Sims (1984), from other cited sources, and from personal observations.

3.1.3 Diagnostic combination

Adults small to medium carabids. Members sharing with other Bembidiini narrow, subconical apical palpomere, lack of dorsal paraörbital groove, separation (in most species) of interval 9 setae into humeral set and apical set. Distinguished from other Bembidiini by possession of lacinia without dorso-apical setae; glossal sclerite bisetose; paraglossal lobes short to moderate in length; clypeus bisetose; elytra with striate or punctatostriate or effaced interneurs, sutural interneur present, but short; recurrent elytral groove absent; seta eo9 lacking; uniperforate procoxal cavities; protibia truncate, not apically notched; protarsomere 1 of male with two rows of transversely apically dilated adhesive setae; internal sac of male aedeagus with brush sclerite.

First instar larva sharing with other Bembidiini egg bursters consisting of denticulate microsculpture on parietale or frontale, single-clawed tarsi, unarticulated urogomphi, which are fused to tergum ten. In addition, setae of dorsal surface generally distally tapered; if not tapered, then bluntly tipped, *not* tipped by two to six projections; seta PR_{13}, ME_{14}, and TE_{11} generally present, abdominal hypopleurites lacking setae; seta TA_1 in proximal one-third of tarsus; coronal suture relatively long (LCl/LHl = .094-.224), not shorter than length of antennomere 1; mandible with cutting edge not denticulate (except slightly so in the two *B. umbratum* examined); galeomere 2 relatively short, less than 1.5 times longer than first article.

Notes on generic recognition.– The subtribe Bembidiina contains four genera in addition to *Bembidion*: *Asaphidion*, *Phrypeus*, *Bembidarenas*, and *Zecillenus*. Adults of *Asaphidion*

(Holarctic) differ from *Bembidion* in lacking striate interneurs, possessing pubescent pronota and elytra, having 6-8 setae on the apex of the glossal sclerite (as opposed to the pair found in *Bembidion*), and having protarsomere 1 of males with small adhesive setae generally distributed, not arranged in two rows (Figs. 87, 89). Adults of *Phrypeus* (western North America) differ in lacking a brush sclerite on the internal sac of male genitalia. Adults of *Bembidarenas* (southern South America) can be distinguished from *Bembidion* by the presence of two pairs of clypeal setae, presence of 6-8 glossal setae, lack of a brush sclerite on the internal sac of male genitalia, and symmetrical parameres. Adults of *Zecillenus* (New Zealand) are distinct from *Bembidion* in lacking a brush sclerite on the internal sac of the male genitalia, in possession of a pronounced subapical elytral sinuation, and in having the basilateral pronotal seta far in front of hind angle (although this latter state is characteristic of several *Bembidion* species from Saint Helena (Basilewsky 1972)).

Bembidion larvae are difficult to distinguish from those of related genera. Among Bembidiini other than *Bembidion*, larvae are known of only a few Tachyina (Cerruti 1939, van Emden 1942, Erwin 1975, Gardner 1938, Kirk 1972, Perris 1862, Stebbing 1914, Thompson 1979, Xambeau 1894) and *Asaphidion* (Bauer 1971, Boldori 1939, Bøving 1911, van Emden 1942, Larsson 1939, Raynaud 1976a, my observations). (I have recently raised larvae of *Polyderis*, a tachyine, and

Phrypeus, but they are as yet unstudied.) The known tachyine larvae have seta TA_1 near or distal to middle of tarsus, in contrast to the more proximally placed TA_1 of *Bembidion*, the tachyine galeomere 2 is relatively long (about two times length of first), and the coronal suture is relatively short (shorter than antenomere 1) (van Emden 1942, Hůrka 1978). More differences will probably become apparent once tachyine larvae are studied in greater detail; sensillar characters are for the most part unexamined.

Many of the characters used by van Emden (1942) to distinguish *Bembidion* from *Asaphidion* do not hold for all species (Andersen 1966, Hůrka 1978). The only single character considered by van Emden (1942), Andersen (1966), and Hůrka (1978) to separate the genera consistently is the size and number of the egg bursters: *Asaphidion* first instar larvae reportedly have a few large tooth-like spikes on the frontale, in contrast to the numerous smaller denticles of *Bembidion* specimens. But even this character is inconstant. The microsculpture on the frontale of *Bembidion* ranges from absent (*B. carinula* Chaudoir, *B. aenulum* Hayward, and others), to low and multipointed (many species, including *B. foveum* Motschulsky, *B. bowditchii* LeConte, and others), to numerous small denticles (many species, including several *Chrysobracteon* species), to a few large teeth (*B. interventor* Lindroth and *B. obtusum* Serville). Denticulate microsculpture is also present on the parietale, near the coronal suture, of all *Bembidion* first instars I have studied, reaching its most extreme form in *B. carinula* (Figs. 228, 234). This parietal microsculpture, as well as any found on the frontale, probably serves an egg-bursting function. First instars of both *Asaphidion flavipes* Linné and *A. alaskanum* Wickham have large frontale teeth *and* prominent denticles on the parietale (Boldori 1939; van Emden 1942:fig. 64; Bauer 1971:158-159; my observations), a condition virtually identical to that found in *B. interventor* and *B. obtusum*. Other characters must thus be sought.

At least four characters can be used to distinguish first instar larvae of all 33 *Bembidion* species I have examined (those characterized in Tables 2, 4, and 5) from the one first instar *Asaphidion alaskanum* at my disposal. The *A. alaskanum* larva has: sensilla MX_{11} and MX_{12} relatively long (longer than a quarter the width of the palpomere to which they are attached; very much shorter in *Bembidion*); setae PR_{13}, ME_{14}, and TE_{11} each replaced by a patch of two to four short, thick setae; abdominal hypopleurites with one seta each (absent in *Bembidion*); most large dorsal setae not distally tapered, instead tipped by a frequently crown-like arrangement of two to six projections (Fig. 195). Apically dilated and crowned setae appear to be present as well in at least first instar *A. flavipes* (Boldori 1939, Bauer 1971:fig. 4), but I cannot judge the uniformity of *Asaphidion* with respect to the first three characters. The diagnosis of *Bembidion* larvae given above is thus tentative.

3.1.4 Description

In the following description of *Bembidion*, I include a number of previously unstudied characters. Chief among these are characters of sensilla. Setation has long been used for taxonomic characters within carabids, but the smaller sensilla of adults have generally been neglected. There is a wealth of small receptors on the surface of carabid adults, particularly on the head (for example, see the studies on antennal sensilla by Juberthie and Massoud (1977) and Daley and Ryan (1979)). The number, position, and types of these sensilla should provide numerous characters for phylogenetic analyses. Goulet (1983), Bousquet and Goulet (1984), and Landry and Bousquet (1984) have already shown the usefulness of some sensilla of larvae for inferring phylogeny, and the same may apply to other larval sensilla and sensilla of adults. I do not by any means attempt to fully describe the sensilla of *Bembidion* specimens, nor exhaust the supply of other characters. Instead, I discuss only some of those characters that appear, based upon previous work and a preliminary examination of cleared specimens of several carabid tribes, to be potentially useful for studies of carabid phylogeny.

Adults small to medium (about 2 to 9 mm in length), generally slender, in many species with relatively narrow forebody.

Color varied, many species dark, concolorous, many others with spotted elytra, or generally pale. Appendages pale yellow to black. Most species have a metallic reflection.

Microsculpture of dorsal surface varied, ranging from close-set transverse lines, giving the surface an iridescent reflection, to granulate isodiametric sculpticells, to absent.

Sensilla. (In this and following descriptions, sensilla of genitalia will be described elsewhere, in the sections "Male genitalia" and "Female genitalia".) Two supraorbital setae. Antennomeres 3-11 pubescent throughout length. Clypeus with one seta near each lateral margin. Labrum with six setae dorsally near apex, more numerous shorter ones ventrally; numerous sensilla of various sorts clothe the surface of the epipharynx; with one cluster of presumed chemoreceptors in a sclerotized patch on either side of epipharyngeal hump (Figs. 24,37). Mandible with one seta in each well-developed scrobe; basomedial brush short, not extended far apically along inner surface of mandible; numerous small sensilla, with three large sensilla on dorsal surface (visible as small open circles in Figs. 25 and 28): these may be large chordotonal organs. Digitiform sensilla (Zacharuk *et al.* 1977, Honomichl 1980, Guse and Honomichl 1980, Honomichl and Guse 1981) arranged in one row near base of last maxillary palp article; tip of maxillary palp with several kinds of sensilla (Fig. 38); three centrally convergent rows of what are probably contact chemoreceptors flanked by a few small clusters of minute sensilla and a few larger possible plate-like organs (observed: *B. balli* Lindroth, *B. foveum*, *B. carinula*, and *B. umbratum* LeConte); palpomere 3 pubescent. Stipes with two long and several shorter setae in most species. Lacinia without dorso-apical setae; dorsal surface with only one to three setal rows (Figs. 42, 43, 46-48). Galea tip with three or four sensillar types, arranged as in Fig. 41 (only studied in *B. foveum*). Terminal labial palpomere without digitiform sensilla, apical sensilla similar in type, but different in distribution to those of maxillary palps (Fig. 39); palpomere 2 with two to five setae on anterior margin. Glossal sclerite with two long subapical setae. One pair of mental setae and 2-5 pairs of submental setae. Pronotum generally with one midlateral and one basilateral seta on each side. Generally two discal setae on elytral interval 3, although *B. quinqestriatum* Gyllenhal has one, *B. laterale* Samouelle four, and a number of species have three setae (Lindroth 1976); occasionally on other intervals as well (especially 5 and 7); elytra not pubescent; basal setiferous pore puncture (ed1) present, as well as one or two preapical discal setae (ed6 and ed7); umbilical series of setae (in interval 9, adjacent to interneur 8) in most species separated into a humeral set (eo1-eo4) and a subapical set (eo5-e08); eo9 lacking [*B. foveum*, *B. argenteolum* Ahrens, *B. semenovi*, and *B. punctatostriatum* Say generally have extra setae between eo4 and eo5; *B. planatum* LeConte generally has an extra seta between eo6 and eo7; members of subgenus *Euperyphus* Jeannel general have one extra seta in the humeral set]. Procoxa without setae, mesocoxa bi- or tri-setose, metacoxa trisetose on ventral surface; pro- and mesotrochanters unisetose; metatrochanter with one ventral seta in addition to several short dorso-basal setae; protarsomere 4 in both sexes of most species with ventroapical projection with four setae, the two central of which are generally apically flattened [projection and setae are lacking in *Asaphidion*, *Phrypeus*, and *Zecillenus*]; male with adhesive squamo-setae (Stork 1980), apically dilated transversely, present in two rows on protarsomere 1, and in one to two rows on protarsomere 2. Males with two major setae on sternum seven, females with four.

Head prognathous, with frontal furrows variously developed, from shallow to deeply incised. Eyes generally moderate to large, and convex, although small in a few subgenera (*Amerizus* Chaudoir, *Tiruka* Andrewes, *etc.*). *Antenna* in most species slender, articles subcylindrical, slightly flattened. *Clypeus* with frontoclypeal suture impressed. *Labrum* as in Fig. 24, subrectangular, with front margin entire. *Mandibles* (Figs. 25, 28-30) falcate; terebral margin thin and cutting, with many regularly spaced pore canals extended to mesal margin (Fig. 31); ventral groove with brush of clumped microtrichia (Figs. 29c, 30c, 32, 33);

right mandible generally with distinct anterior and posterior retinacular teeth, terebral tooth, premolar, and molar; left mandible with short retinacular ridge, and distinct premolar and molar; molars on both mandibles thin, only slightly sclerotized, sharply pointed (Figs. 32, 33). *Maxilla* (Fig. 26) with small, subulate, subconical palpomere 4; galeomeres subequal in length (articles fused in *B.* (*Amerizus*) *wingatei* Bland); galeomere 2 with groove for reception of lacinia; lacinia in most species generalized, without microsculpture. *Labium* (Fig. 27) with palpomere 3 small, subulate, subconical; paraglossal lobes thin (but not nearly as thin as those of trechines), rounded; short to moderate in length; with short microtrichia; glossal sclerite broad and flat. Mentum with single tooth; epilobes usually distinct; mental pits absent. Mentum and submentum distinct, except in members of *Ocys* Stephens.

Prothorax with closed, uniperforate coxal cavities. Pronotum shape varied, from cordate to subcircular to trapezoidal. *Mesothorax* broadly connected to prothorax, with conjunct-confluent coxal cavities. Scutellum visible externally, moderate in size. *Metathorax* with disjunct-lobate, confluent coxal cavities.

Elytron generally with nine punctatostriate interneurs, in many species effaced laterally or posteriorly; sutural interneur short; recurrent groove absent, although apex of interneur 5 sulcate in some species; subapical plica present (most species, Fig. 67) or absent (*B. aenulum* Hayward and *B.*

sp. nr. *aenulum*, Fig. 65); if present, then as typical for carabids, a simple, curved ridge on the undersurface of the elytron below setae eo7 and eo8, in most species merged with the elytral margin.

Metathoracic wing present, full, or variously reduced; if well-developed, then wedge cell a thin triangle or absent (Fig. 74); oblongulum cell elongate.

Legs long and slender in most adults. Groove in coxa for reception of metafemur restricted to posterior margin of coxa. Protibia anisochaetous, with distinct antennal cleaner ("Grade B" (Hlavac 1971)). Protarsus with first two to three articles slightly expanded in male, with apico-lateral projections. Unguitractor plate present, plate-like. Tarsal claws simple, untoothed.

Abdomen with wing-folding spicule patches on abdominal sterna I and VI, as well as front of VII.

Male genitalia with styliform parameres (Figs. 180, 181), the right smaller than the left; parameres with 1-5 apical setae; ring sclerite as in Fig. 182. Basal bulb of median lobe with most of right wall lacking; internal sac with brush sclerite (Figs. 99-102, 107) (except in a few species of subgenera *Antiperyphanes* Jeannel and *Chilioperyphus* Jeannel (Jeannel 1962)), often with numerous other sclerites; flagellum often present, of varied shapes. Right and left testes equally developed.

Female genitalia with sclerotized spermatheca (except in the subgenera *Synechostictus* Motschulsky, *Amerizus*, *Tiruka*, *Pseudolimnaeum* Kraatz (Perrault 1981)), connected to bursa copulatrix by spermathecal duct; duct in many species with a sclerotized base, called the sclerotized vaginal plate (in coccinelids, a similar structure is referred to as the infundibulum (Gordon 1985)); spermathecal gland present, with subbasal portion enlarged and annulated; spermatheca lying in right side of abdomen (Fig. 145; Schuler 1960, Erwin and Kavanaugh 1981, Perrault 1981). Two stylomeres, second spatulate; first stylomere (S1) asetose or setose; second stylomere (S2) with zero to five or more dorsolateral ensiform and one dorsomedial ensiform setae, in addition to two nematoid setae and several furrow peg sensilla in sensory furrow, and numerous scattered chordotonal organs. Seven to ten ovarioles per ovary (Robertson 1961).

Internal structure. Nervous system with first abdominal ganglion fused to last thoracic ganglion; second through seventh abdominal ganglia fused together (Ali 1967; I have confirmed this as well for one *B. lorquinii* Chaudoir female). Proventriculus (Figs. 188, 189) with four similar, inwardly directed lobes, each lobe with patch of stout, posteriorly directed scales at anterior end, and a tubercle-studded sclerotized lobe at posterior end; in between is a membranous region of posteriorly directed microtrichia; the exact pattern varies considerably between species (observed in *B. carinula*, *B. levettei* Casey, *B. harpaloides* Serville, and *B. wingatei*). Six oval or circular rectal sclerites, arranged in one circle around circumference of rectum (Fig. 183; observed in several *Chrysobracteon* species, as well as *B. coxendix* Say, *B. confusum* Hayward, *B. chalceum* Dejean, *B. aeneicolle* LeConte, and *B. viridicolle* La Ferté). Prothoracic muscle M15 three-parted, with M15b connected to M15c (Baehr 1979; see that paper for further description of prothoracic musculature). Origin of muscle M3 of female abdomen at caudal end of tergum VIII (Bils 1976; see that paper for more information about female abdominal musculature).

Pygidial defense glands (Fig. 184) paired, consisting of a long secretory duct, large, ovoid reservoir, and a pleated exit tube exiting laterally in membranous dorsum anterior to tergum IX/X. Defense secretion consisting of aliphadic ketones, higher saturated acids, and aromatic aldehydes, secreted by oozing (Schildknecht *et al*. 1968, Moore 1979).

Chromosomes about 24 in number (male 2n=22+XY in most species); sex chromosome system XY/XX or XO/XX (Smith 1960; Rożek 1981; Serrano 1981a, 1981b, 1984; Maddison 1985). Male meiosis achiasmate, lacking typical diplotene (Serrano 1981c, Maddison MS).

Egg of *B. confusum* briefly described by Silvey (1935).

Larva generalized, without striking modifications. The following description is based on examination of 35 species in my collection as well as the brief published descriptions of *Bembidion* larvae (Andersen 1966; Bauer 1975; Bøving 1911;

van Emden 1942; Jeannel 1941; Larsson 1941, 1968; Kirk 1972; Lindroth 1955, 1980; Netolitzky 1926; Raynaud 1976b, 1977; Rey 1887; Rye 1908; Schaum 1859; Schiødte 1867; Silvey 1935; Smrž 1979; Thompson 1979; Uéno 1955).

First instar *size*. LHw = 240-605 µm, LHl = 240-570 µm.

Microsculpture. Parietale with denticulate microsculpture near coronal suture, probably serving an egg-bursting function (Figs. 226-231). Frontale posteriorly with microsculpture absent, or low, multitoothed combs, or consisting of numerous or few small denticles, or a few large denticles (Figs. 226-231); the frontal microsculpture probably also serves an egg-bursting function.

Sensilla. Number and position of setae and chordotonal organs ("pores") are as inferred by Bousquet and Goulet (1984) to be the ancestral carabid state, except as noted below. Frontale with extra small sensillum (Fig. 205) between or near FR_8 and FR_9; this sensillum is present in many carabids, including *Opisthius*, *Elaphrus*, *Patrobus*, *Pterostichus*, *Platynus*, and *Harpalus* larvae, and perhaps should be added to the hypothesized ancestral complement. Antenna (Fig. 201) with sensorial appendage prominent and basally constricted. Chordotonal organ MXc of maxilla (Fig. 203) equidistant from MX_2 and MX_3; setal group gMX with only one to two rows of setae; MX_{11} and MX_{12} very small, conical (similar to FRf, Fig. 204). Digitiform sensilla on maxillary palpomere 4 arranged in one subapical row around circumference of article (Fig. 206); apical sensilla of palpomere as in Fig. 206. Galea apically with four apical sensilla (Fig. 207), in same pattern as found in *Nebria* (Spence and Sutcliffe 1982). Labium (Fig. 202) with LA_5 on glossal projection, which is therefore quadrisetose (Fig. 209); digitiform sensilla arranged irregularly laterally on apical palpomere near base (Fig. 208); apical sensilla as in Fig. 208. Many long setae covered with short projections emerge from the mouth cavity over the labium (Fig. 202), similar to setae found in *Omophron* (Landry and Bousquet 1984) and many other carabids (my observations). Chordotonal organs PRh, PRi, and PRj absent from pronotum. Mesothorax with chordotonal organs MEd and MEe absent. Metathorax lacking seta ES_1. Legs with seta FE_2 shorter and thinner than other setae on femur. Abdomen with TEb absent from all segments; seta TE_3, TE_4, TE_5 present on first segment; TE_5 and one of TE_3 or TE_4 absent from all other segments. First abdominal sternum with ST_5 absent; all sterna without setae on hypopleurites.

Head (Figs. 194, 210-217, 219-224) with postorbital groove shallow or absent, occipital groove shallow. Nasale varied, denticulate (Figs. 192, 193, 238). Six stemmata on each side (apparently absent in *B. obtusum*). Mandible (Figs. 198-200) with single retinacular tooth, and penicillus; mesal margin not denticulate anterior to retinacular tooth (except slightly denticulate in the two *B. umbratum* examined). Maxilla as in Fig. 203, without remnant of lacinia; palp with three articles, none subdivided.

Galeomere 2 narrow, elongate, 1 to 1.5 times length of galeomere 1. Labium as in Fig. 202, palp with two articles, none subdivided; palpomere 2 elongate and narrow.

Thorax. Prothorax and metathorax lacking spiracles; spiracles present on mesothorax.

Leg with only one claw.

Abdomen. Abdominal segments I through VIII with spiracles. Urogomphus not articulated, fused to tergum IX.

Second and third instar larva with characters of first instar, but with setae more numerous on most body sclerites. Body sparsely covered with very short setae, in addition to the more evident, long setae. Stipes with three or four setae on outer margin. Egg bursters absent. Cervical groove more prominent than in first instars, head less constricted basally (Fig. 218). Antennae and maxillae more elongate than in first instars.

Pupa known only in *B. confusum*; for a brief description, see Silvey (1935).

3.2 Subgenera and subgeneric groups of *Bembidion*

The genus *Bembidion* is divided into a large number of subgenera or species groups. Only a few attempts have been made to join these subgeneric taxa into more inclusive natural groups. Netolitzky (1942, 1943) recognized several divisions within *Bembidion*. Species with an angulate humeral margin (including *Chrysobracteon*) were separated from those with an evenly prolonged or absent margin; in the latter group he proposed two major series, divided between species with ed3 and ed5 attached to interneur 3 (the "*Peryphus*-Reihe"), and those with ed3 and ed5 in interval 3, unattached to an interneur (the "*Notaphus*-Reihe"). Jeannel (1941) divided *Bembidion* more finely, into seven phylogenetic series: the *Ocys*, *Cillenus*, *Notaphus*, *Bembidion*, *Peryphus*, and *Odontium* series. The *Odontium* series contains four taxa, ranked by Jeannel as genera, namely *Phyla*, *Metallina*, *Hydrium*, and *Odontium*, linked by common possession of angulate humeral margin. His genus *Odontium* includes a number of subgenera, among them *Chrysobracteon*, that appear closely related. I include the taxon within *Bembidion*, and call it the "*Odontium* subgeneric group". The group comprises three subgenera from the northern hemisphere. Before discussing it in detail, I will mention two subgenera perhaps related to the *Odontium* group.

3.3 Subgenus *Microserrullula* Netolitzky

Serrula Netolitzky, 1910:209 (not Mörch 1853).

Microserrullula Netolitzky, 1921:185. [Type species *Bembidion aegyptiacum* Dejean, designated by Jeannel 1941:540.]

Darlington (1959) suggested that the Oriental-Ethiopian subgenus *Microserrullula* may be related to *Odontium*. *Microserrullula* contains about thirteen species, ranging from Laos and India north into the Caucasus, west into Africa, and as far south as Madagascar (Andrewes 1935, Netolitzky 1942, Schuler 1959, Basilewsky 1968). Members of the subgenus are characterized by a number of apomorphies, including: possession of serrulate elytral margin; prominent suborbital ridge; broad pronotal base; very long flagellum of male genitalia; long, multiply coiled spermathecal duct.

In general appearance *Microserrullula* specimens greatly resemble members of *Odontium*, especially with the prominent and angulate shoulder margin, large size, broad pronotum, and full punctatostriate elytral intervals. However, I cannot clearly interpret these characters phylogenetically; genitalic character states in *Pseudoperyphus* that suggest relationship with the *Odontium* group are not present in *Microserrullula*, but the states of *Microserrullula* may simply be autapomorphies. Proper placement of the subgenus awaits more detailed study, especially of first instar larvae. *Microserrullula* may belong in this group, but I will exclude it from subsequent analyses because of the uncertainty.

3.4 Subgenus *Pseudoperyphus* Hatch

Pseudoperyphus Hatch, 1950:100. [Type species *Bembidion chalceum* Dejean, by original designation.]

Bracteomimus Lindroth, 1955:49. [Type species *Bembidion chalceum* Dejean, by original designation.]

Subgenus *Pseudoperyphus* Hatch may be closely related to the *Odontium* subgeneric group. It contains at least six North American species (*B. chalceum* Dejean, *B. antiquum* Dejean, *B. honestum* Say, *B. integrum* Casey, *B. rufotinctum* Chaudoir, and one undescribed species, herein called *B. "sp.17"*); I am presently revising the group. Adults differ from the *Odontium* subgeneric-group by lack of an angulate humeral margin, and by possession of an exceptionally thick ventral margin of the right lobe of the central sclerite complex of the internal sac of the male genitalia. The first stylomeres of females have numerous (eight or more) long setae (as long or longer than those of *B. stenoderum* Bates, see Fig. 152), a state I have seen elsewhere only in *B. (Hirmoplataphus) concolor* Kirby. First instar larvae lack a frontal spot pattern and have a relatively unconstricted neck. Members are found on gravel-dominated shorelines. In spite of these differences, the construction of the male internal sac and spermatheca are essentially identical to those of *Chrysobracteon* and its relatives, and some relationship may be indicated. I will discuss *Pseudoperyphus* further in my phylogenetic analyses.

3.5 The *Odontium* subgeneric group

Recognition.– Members of the *Odontium* subgeneric group are generally large *Bembidion* (SBL = 3.3-7.1mm, generally over 4.5mm), inhabiting sand or silt shores of creeks, rivers, and lakes. Internal sac of male genitalia strikingly uniform in pattern, consisting of large dorsal plate, central sclerite complex with right lobe and long flagellum, and relatively small ventral sclerite patch of two basins, as in Figs. 112-128. In females, S1 is setose, without sclerotized plate at base of spermathecal duct. The humeral margin is angulate; interneur 5 is not apically sulcate, with the adjacent outer interval not ridged; elytra unspotted by pigment. Larvae generally have three-spotted frontale (Figs. 215, 216, 219), with posterior part of the wide head constricted, and short coronal suture [for the *Odontium* subgeneric group, LCl/LHl=.094-.196 (excluding *B. aenulum*, .094-.161), mean=.129 (n=16 species, 42 specimens); for other *Bembidion*, LCl/LHl=.154-.224, mean=.184 (n=16 species, 20 specimens)].

I have been able to resolve the subgeneric group members I have studied into six clearly defined clades of two or more species, as well as six single species (see Fig. 277); evidence will be provided in "Cladistic structure of the near relatives of *Chrysobracteon*". I have not been able to group these twelve lines much further into more-inclusive monophyletic or paraphyletic assemblages.

Two of these clades are generally considered distinct subgenera: *Chrysobracteon*, with 17 species; *Ochthedromus*, with 3 species. The remainder of the subgeneric group is placed within subgenus *Odontium*; some authors remove from *Odontium* subgenus *Bracteon* (for example, Lindroth (1963)), but I prefer to follow Jeannel (1941), and not recognize the distinction. I also include within *Odontium* the four members of *Cylindrobracteon* Netolitzky; Kryzhanovskij (1983) did this as well. I will discuss these decisions further under the account of subgenus *Odontium*.

New subgeneric names could be proposed for clades such as the *B. confusum* + *B. arizonae* + *B. sculpturatum* group, but this is quite unnecessary at present and would only add unneeded names to the literature. I will not radically alter existing subgeneric classification; such changes await more detailed study of the group.

3.5.1 Key to adults of the *Odontium* subgeneric group

1. Setae in elytral interval 3 surrounded by a distinct, dull patch, which has deeper microsculpture lines and is therefore more granulate than the rest of the elytron...*Chrysobracteon*

1'. Elytral interval 3 with more uniform microsculpture.......................................2

2(1'). Setae ed3 and ed5 in elytral interval 3 in large foveae; pronotal base markedly constricted; submentum with more than eight long setae...*Ochthedromus*

2'. Elytral intervals lacking foveae, or, if foveae present (*B. foraminosum* Sturm), then pronotum less constricted (similar to Fig. 6); submentum with six or less long setae........................*Odontium*

3.6 Subgenus *Ochthedromus* LeConte

Ochthedromus LeConte, 1848:453. [Type species *Bembidion americanum* Dejean, designated by Lindroth (1963).]

Diagnostic combination.– Adult with protruding eyes; submentum with transverse row of about 10 long setae, suborbital setae especially long; pronotum with constricted base, and markedly rounded sides; humeral margin angulate; elytra with foveae at bases of ed3 and ed5; interneural punctures small; male internal sac with markedly sclerotized strip inward of ostium: a similar sclerotized strip occurs in some other *Odontium* subgeneric group members, but in *Ochthedromus* specimens the strip has a papillate appearance, as if composed of numerous minute beads. **Larva** known of *B. cheyennense* Casey; with three-spotted frontale; other characters listed in Table 5.

The group is probably monophyletic. Lindroth considered it as consisting of two species, *B. bifossulatum* LeConte and *B. americanum* Dejean. However, my studies indicate that *B. bifossulatum* consists of two distinct forms, separable on the basis of the mentum teeth and male genitalia. As they are important for my discussions of *Chrysobracteon* phylogeny, a clarification of their nomenclature is warranted.

The western form has a rounded, somewhat-trapezoidal, laterally ridged mentum tooth, with distinct epilobes (Fig. 58); the ostial sclerotized strip in the male internal sac is abruptly bent. The eastern form has a rectangular, truncate, bulbous mentum tooth, with somewhat indistinct epilobes (Fig. 57); males have a more gently curved ostial sclerotized strip. In the material at hand, the two forms appear allopatric. However, I have not studied much material, and further study may reveal sympatry with or without evidence of gene flow. I am uncertain as to whether to consider them separate species or subspecies; nonetheless, distinct names are warranted, and herein I will treat them as species. The types of three names belong to the western form (*B. bifossulatum* LeConte 1851 (holotype female, MCZ!), *B. regestum* Casey 1918 (lectotype male, USNM!), and *B. ferreum* Casey 1924 (lectotype female, USNM!)), with *B. bifossulatum* LeConte being the valid name. The types of three names belong to the eastern form (*B. cheyennense* Casey 1918 (lectotype male, USNM!), *B. sufflatum* Casey 1918 (lectotype male, USNM!), and *B. nuperum* Casey 1918 (holotype male, USNM!)); I herewith choose *B. cheyennense* Casey as the valid name.

Species included

B. cheyennense Casey, 1918:15. (AZ,CO,WY,AB,SA, and eastward) !

B. bifossulatum LeConte, 1851:186. (CA,ID,BC) !

B. americanum Dejean, 1831:87. (U.S.A., Canada) !

3.7 Subgenus *Odontium* LeConte

Odontium LeConte, 1848:452. [Type species *Bembidion coxendix* Say, by original designation.]

Bracteon Bedel, 1879:27. [Type species *Bembidion striatum* Fabricius, designated by Jeannel (1941)]

Cylindrobracteon Netolitzky, 1940 or 1942:50. [Type species *Bembidion fusiforme* Netolitzky, by original designation.]

Diagnostic combination.– Adult with characters of the *Odontium* subgeneric group; silver spots lacking; elytra around ed3 and ed5 generally without foveae; if foveae present, then submentum with six or less long setae.

Odontium is often split into two or three subgenera, but the distinction between them seems rather slight. *Bracteon* has been removed because of the wide interval 9 (as wide as 8), and the shallow interneur 8 in front of middle (Lindroth 1963:242), and mouthpart structure (Netolitzky 1942:49). The elytral characters, however, are not at all clear, with several species (for example, *B. robusticolle* Hayward, *B. carinatum* (LeConte), and *B. durangoense* Bates) showing intermediate states. Fig. 1 illustrates the lack of two distinct groups in the *Odontium-Bracteon* complex based on the relative widths of intervals 8 and 9. As well, mouthpart structure is more uniform across the group than supposed by Netolitzky: only *B. confusum*, *B. sculpturatum*, and *B. arizonae* have distinctive mandibles and laciniae.

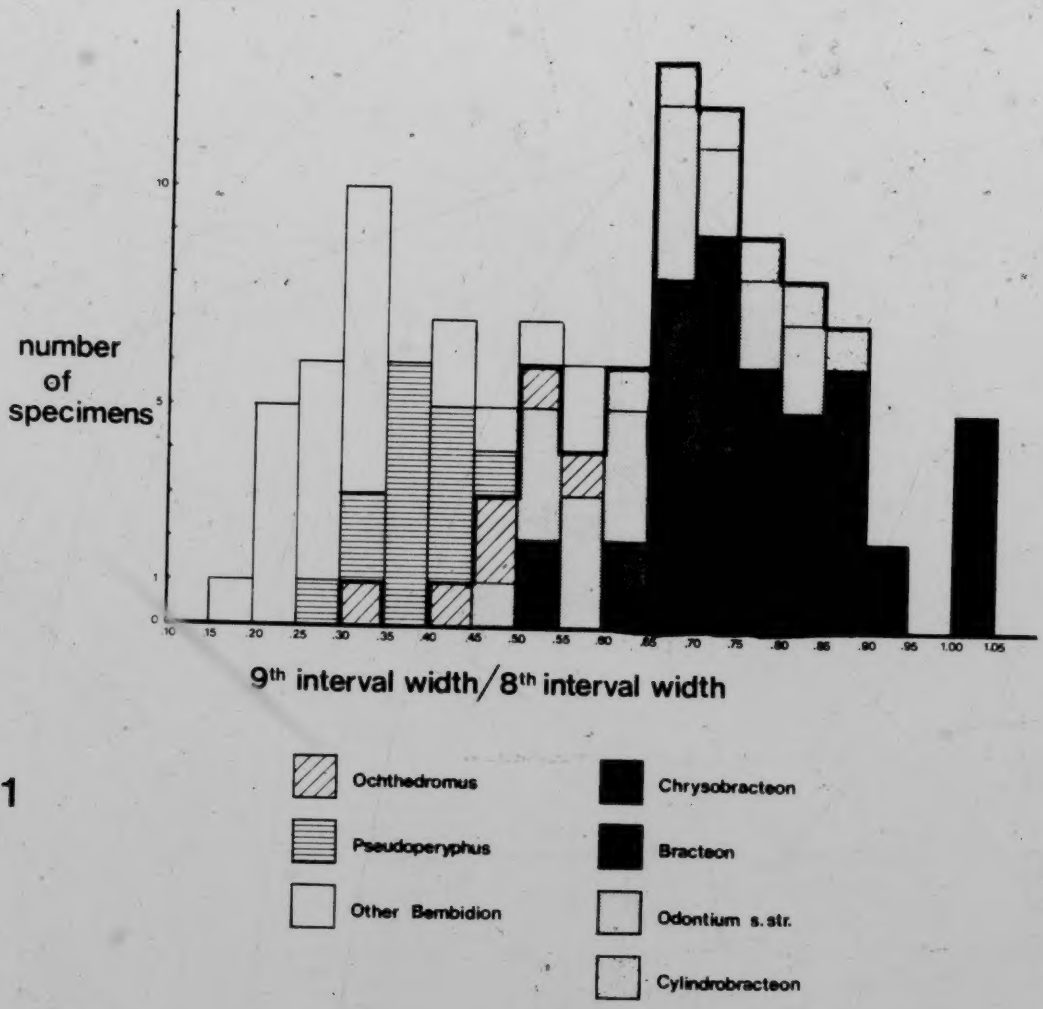
Four East Asian species are occasionally separated as a separate subgenus, *Cylindrobracteon*. The only known distinctive character of the group is the fusiform body, with pronota that are trapezodial, with broad base (extended outward to humeral angles), nearly straight margins, and protrudent, almost-divergent front angles. As well, the midlateral pronotal seta is absent, and the humeral margin is long, but these latter traits are shared with a number of *Odontium* (*s.str.*) species. The North American species *B. aenulum* and *B.* sp. nr. *aenulum* are two such species, and their pronota are somewhat intermediate between those of *Cylindrobracteon* and other *Odontium* (*s. str.*). Following Kryzhanovskij (1983), I do not consider *Cylindrobracteon* distinctive enough to warrant subgeneric status.

Until *Odontium* is better understood phylogenetically, I will treat the species as belonging to one subgenus.

Odontium comprises all species of the *Odontium* subgeneric group other than *Ochthedromus* and *Chrysobracteon*. As it stands, it may be paraphyletic, with *Ochthedromus* or *Chrysobracteon* derived from it, although I have no evidence for or against this.

Figure 1. Histogram of ratio (interval 9 width)/(interval 8 width) of studied *Bembidion* species.

Two or three specimens measured of most species. Included are all *Bembidion* species of Tables 2, 4, and 5. Results for *Odontium* subgeneric group members are enclosed by a thick black line. The divisions between *Bracteon*, *Odontium*, and *Cylindrobracteon* are those recognized by Netolitzky (1942) and Lindroth (1962); note that I include all three within subgenus *Odontium* (see discussion in text).


number of specimens
0
1
5
10
.10
.15
.20
.25
.30
.35
.40
.45
.50
.55
.60
.65
.70
.75
.80
.85
.90
.95
1.00
1.05
9th interval width/8th interval width
Ochthedromus
Pseudoperyphus
Other Bembidion
Chrysobracteon
Bracteon
Odontium s. str.
Cylindrobracteon

1

North American and western Palearctic members of the subgenus appear well-understood (except for one undescribed species in southern U.S.A.), but material from the eastern Palearctic region is in need of study.

Note that "*Bembidion bowditchi*" is an incorrect subsequent spelling of *Bembidion bowditchii* LeConte (see ICZN, Third Edition, Article 33(d)).

Species included (for some synonyms, see Lindroth (1963), Erwin (1984))

B. bowditchii LeConte, 1878:451. (WY,ID,WA,BC) !

B. foraminosum Sturm, 1825:183. (Europe) !

B. striatum (Fabricius), 1792:179. (Palearctic) !

B. suturale Motschulsky, 1850:16 (Caucasus)

B. persimile Morawitz, 1862:225. (Japan, north-eastern China) !

B. gebieni Netolitzky, 1928:168. (China)

B. kaszabi Jedlička, 1961:311. (Japan)

B. japonicum Jedlička, 1961:311. (Japan)

B. soederbomi Jedlička, 1965b:203. (Mongolia)

B. robusticolle Hayward, 1897:50. (U.S.A.) !

B. coxendix Say, 1823a:151. (U.S.A., Canada) !

B. carinatum (LeConte), 1851:186. (CA,AZ) !

B. sculpturatum (Motschulsky), 1859:132. (CA,NV,WA) !

B. confusum Hayward, 1897:52. (U.S.A., Canada) !

B. arizonae Lindroth, 1962:246. (AZ, Mexico) !

B. durangoense Bates, 1891:263. (AZ, Mexico) !

B. aenulum Hayward, 1901:156. (IW, NK) !

B. sp. nr. *aenulum*. (MS, MO) !

B. aeneipes Bates, 1883:276. (Japan, China) !

B. fusiforme Netolitzky, 1914b:168. (Formosa, Japan) !

B. subfusum Darlington, 1959:335. (Philippines)

B. chloropus Bates, 1883:277. (Japan) !

3.8 Subgenus *Chrysobracteon* Netolitzky

Bembidion sensu LeConte 1848, *nec* Latreille.

Chrysobracteon Netolitzky, 1914a:166. [Type species *Bembidion velox* (Linné) or *B. litorale* (Olivier); see "Notes on the type species of *Chrysobracteon*", below.]

Parabracteon Notman, 1929:157. [Type species *Bembidion tuberculatum* Notman (= *B. carinula* Chaudoir), by monotypy.]

Litoreobracteon Netolitzky, 1940 or 1942:51. [Type species *Bembidion litorale* (Olivier), by original designation.]

Argyrobracteon Netolitzky, 1940 or 1942:53. [Type species *Bembidion argenteolum* Ahrens, by original designation.]

Conicibracteon Netolitzky, 1940 or 1942:53. [Type species *Bembidion stenoderum* Bates, by original designation.]

Stylobracteon Netolitzky, 1940 or 1942:53. [Type species *Bembidion baikaloussuricum* Netolitzky, by original designation.]

Foveobracteon Netolitzky, 1940 or 1942:54. [Type species *Bembidion foveum* Motschulsky, by original designation.]

3.8.1 Notes on the type species of *Chrysobracteon*

Netolitzky (1914a), in erecting *Chrysobracteon*, did not explicitly include any species. Thus, the "originally included nominal species", from which the type must be chosen (ICZN Third Edition, Article 69), are to be sought in the first publication to place species within the subgenus. The earliest such publication I have found is Müller (1918); he includes within the subgenus *B. litorale*, *B. argenteolum*, *B. foveum*, *B. velox*, and *B. lapponicum* Zetterstedt. Three subsequent papers contain what might be considered type species designations of *Chrysobracteon*: Netolitzky (1940), Jeannel (1941), and Netolitzky (1942). Netolitzky (1940) designates *B. velox* as the type species; but as I discuss in the "Names of taxa" section of "Materials and Methods" (p. 17), that paper may not be a valid publication. Jeannel's (1941:542) statement "type: *littorale* Ol. (prem. désig.)." constitutes a type designation (ICZN Third Edition, Article 69(a)(iv)). Netolitzky (1942) later clearly states the type to be *B. velox*. Both *B. litorale* and *B. velox* are "originally included species", and thus might serve as the type. If Netolitzky (1940) is considered a valid publication, then *B. velox* is the type; if not, then the type is *B. litorale*. A choice awaits the decision regarding status of Netolitzky (1940).

3.8.2 Notes on synonymy

Andrewes (1935), Lindroth (1963), Erwin and Kavanaugh (1981), and Erwin (1982) avoid use of subgeneric names, and use instead more informal species-group names for groupings within *Bembidion*. If this practice were followed for *Chrysobracteon*, it could be referred to as the *B. inaequale*-group, as Lindroth (1962) did for the Nearctic fauna, or, perhaps more appropriately for the world fauna, the *B. velox*-group (as *B. velox* may be the type and is the oldest species name of the group (ICZN Third Edition, Article 6)).

3.8.3 Characterization of *Chrysobracteon*

Adult

Diagnostic combination.– Most easily recognized by possession of two "silver spots" on each elytron, that is, with a distinct patch of granulate microsculpture surrounding ed3 and ed5 (Figs. 5 to 23, 61). Most species have as well dark, shiny patches of weaker microsculpture on the elytral disc; these are termed "mirrors" (Figs. 7 to 23). Other character states as for *Odontium* subgeneric group.

Description.– *Size.* Relatively large *Bembidion*, SBL = 4.4-7.1 mm.

Color. Body black or piceous, unspotted by pigment (although variation in microsculpture and metallic sheen produces a spotted pattern). Generally with metallic reflection (except in some black, presumably old and worn specimens), ranging in color from reddish, to coppery, golden, aeneous, green, blue-green, or bright blue. At least some parts of appendages paler, either testaceous, rufotestaceous, or rufous.

Microsculpture. For the most part isodiametric on dorsal surface, although slightly transverse in some

B. hesperium Casey.

Sensilla. Basilateral seta of prothorax at hind angle. Setae ed3 and ed5 in third interval, not attached to interneur; ed4 absent; eo1 generally far in front of e02-eo4. Protarsomere 4 with ventroapical setae present, narrowly or widely separated.

Thorax. Pronotum with tubercle between basilateral fovea and side margin.

Elytral interneurs punctatostriate, including 8 and 9; interneurs 2 and 3 generally deepened and with larger punctures around silver spots (most extreme in *B. hesperium*); interneur 8 more shallowly impressed anteriorly than 7, interval 8 relatively wide (Fig. 1). Elytral margin angulate at humerus; humeral margin reaching interneurs 4 to 6.

Male genitalia. Internal sac with large dorsal plate; with central sclerite complex consisting of right and left lobes, both moderate to large, as well as a short to medium-length flagellum; with a ventral sclerite patch of two basins separated by a ridge (Fig. 99). Parameres with a varied number of setae, but generally trisetose (for example, of the 102 parameres of *B. lapponicum* studied, 62 had three apical setae, and 37 had four).

Female genitalia. Spermatheca sclerotized, with a distinct ringed cornu; cornu without prominent apical indentation (Figs. 165-179). Spermathecal duct relatively short, with only a few turns and coils, not multiply coiled

(Fig. 145). Sclerotized plate at base of spermathecal duct absent. Female basal stylomere (S1) setose (except in *B. carinula*, members of which have a few minute peg-like sensilla in place of setae).

Chromosomes. Male 2n=20+XY or 22+XY; chromosomes of normal size for *Bembidion* (autosomes 1.2-2.5 μm), submetacentric or metacentric (Maddison 1985:fig. 1).

Larva

Key to larval instars of ***Chrysobracteon***

1. Parietale with denticulate microsculpture near coronal suture (Figs. 226 to 231). Stipes with two setae on outer margin..................first instar

1'. Parietale with microsculpture near coronal suture consisting of shallow meshes or scales, not denticulate. Stipes with three setae on outer margin. Cervical groove prominent................2

2(1') Head capsule narrower (LHw = 510-750 μm); stipes of maxilla relatively short and wide (length/width = 2.50-3.05)............................second instar

2'. Head capsule wider (LHw = 630-1040 μm); stipes of maxilla relatively long and thin (length/width = 3.22-3.89)............................third instar

Diagnostic combination.— Not yet distinguishable as a group from members of subgenera *Odontium* and *Ochthedromus*; the description below applies equally well to the known *Chrysobracteon*, *Odontium* and *Ochthedromus* larvae.

First instar description.– *Size*. LHw = 330-505 μm, LHl = 255-390 μm.

Color. Frontale generally with one central dark spot, and one elongate dark patch on either side of the posterior portion of the frontale (Fig. 215); parietale in several species with dark patch on each side posteriorly near coronal suture (Fig. 215). Some species (*B. balli*, *B. foveum*) with these patches partly masked by generally dark ground color; others (*B. argenteolum*, *B. alaskense* Lindroth, *B. carinula*, and *B. lapponicum*) without distinct patches, having only diffusely darker head center or uniformly dark head.

Microsculpture. Frontale without a row of a few large denticles; with or without a posterolateral patch of small denticles or multi-toothed combs. Parietale with smooth patch mostly lacking microsculpture between FR_4, FR_7, FR_8 and the frontal suture (with a few denticles in *B. punctatostriatum*); generally with denticulate microsculpture laterally.

Head. Head capsule constricted posteriorly; coronal suture short (LCl/LHl mean=.127, n=11 species, 35 specimens).

Second instar description.– As for *Bembidion*, plus: Stipes with three setae on outer margin.

3.8.4 Species included

Chrysobracteon includes 17 known species, ranging throughout the temperate, cold-temperate, and subarctic regions of the northern hemisphere. Delimitation, identification, and description of these species are dealt with later, in the section "Species of *Chrysobracteon*" (p. 75).

One Chilean *Bembidion* species, *B. chlorostictum* Reed (1874), was included in the subgenus by Csiki (1928). Reed (1874), Netolitzky (1931), and Lindroth (1962) considered the Chilean species to be unrelated to *Chrysobracteon* as elytral interval 8 merges with 9 posteriorly as in notaphoid *Bembidion*, in contrast to the presumably primitively separated intervals 8 and 9 of *Chrysobracteon*. However, *B. chlorostictum* shares with *Chrysobracteon* "discoloured shining streaks on the third elytral interstice" (Reed 1874); that is, shallowly microsculptured mirrors. Reichardt (1977) maintains *B. chlorostictum* within *Chrysobracteon*, citing Jeannel (1962) as an authority for this action. As Perrault (1981:245) notes, Reichardt was in error in attributing to Jeannel (1962) the return of *B. chlorostictum* to *Chrysobracteon*, as the species was not mentioned in Jeannel's work. Indeed, Jeannel (1962:536) states, "Quant aux séries phylétiques d'*Ocys*, de *Cillenus*, de *Bembidium*, d'*Odontium*, d'*Asaphidion* définies dans la Faune de France, elles n'ont aucun représentant dans l'hémisphère austral", indicating that he does not believe *Chrysobracteon* (a taxon he includes within *Odontium*) occurs in South America.

I could not locate type material of *B. chlorostictum*. D.H. Kavanaugh informs me (pers. comm. 1984) that no authentic *B. chlorostictum* specimens could be found in the Reed collection at the California Academy of Sciences. I have thus not seen specimens that I can definitely assign to *B. chlorostictum* Reed, nor to my knowledge has any recent carabidologist, but I suspect, as does Perrault (1981), that *B. chlorostictum* is related (if not identical) to *B. (Notaphiellus) cupreostriatum* Germain.

I have examined two unidentified species of *Notaphiellus* (MCZ!), both from Chile. They possess distinct *mirror* patches around ed3 and ed5 (not silver spots); the elytra are a patchwork of mirrors and more deeply microsculptured areas. The male genitalia of the one specimen I studied is clearly "notaphoid", with a large, doubled, scaled ventral sclerite patch; form of internal sac structures is very similar to some North American *Notaphus* such as *B. graphicum* Casey. *B. chlorostictum* Reed is probably also of notaphoid stock, and not a *Chrysobracteon*.

3.8.5 Natural history

Our knowledge of *Chrysobracteon* natural history is rather meager, and can be briefly summarized.

They are shoreline insects, spending most of their lives on vegetationless or sparsely vegetated beaches. In general, they occur on sandy substrates, which may or may not contain fine-grain silts and clays. This uniformity of broad habitat requirements allows rich *Chrysobracteon* communities along some watercourses: I have found six species (*B. balli*, *B. foveum*, *B. carinula*, *B. lapponicum*, *B. punctatostriatum*, *B. levettei carrianum*) in company of related *B. coxendix* and *B. cheyennense* on the barren shores of the North Saskatchewan River near Paynton, Saskatchewan (Fig. 190), and occurrence of four or five species together is not uncommon (Lindroth 1962, my observations). Most shores inhabited by *Chrysobracteon* have at least two species. The means by which these ecologically and phylogenetically similar species coexist in an apparently uniform habitat is uncertain, but a closer examination of the animals and their habitats reveals a greater ecological diversity than is at first evident.

Lindroth (1945) and Andersen (1970) have shown that each European species prefers slightly different habitat substrates. On several beaches in North America, adults of different species were generally found in different microhabitats (my observations). Along the North Saskatchewan River near Paynton, for example, *B. foveum* is commonest around the clay-mixed banks of backwater pools (but many specimens are found along the river shore); *B. balli* and *B. lapponicum* on wet sand close to the river shore; *B. levettei carrianum* on wet sand along the river shore and backwater pool shores; *B. carinula* on sand, including the dry, wind-blown sand of the upper banks as well as along the river shore; *B. punctatostriatum* only on hot, dry sand more than 10 m from the river. These patterns appear to hold throughout the range of each species, but the North American species have not been studied in detail; my data are based on passing observations, lacking careful measurements. I have not collected most of the other species extensively enough to discover microhabitat preferences, but ranges of two other species are nonetheless quite clear: *B. inaequale* is found on clay-mixed sand, usually with a sparse cover of vegetation, around shores of creeks, rivers, and lakes; *B. zephyrum* is restricted to wind-blown sand beaches of the Pacific Ocean.

Behavioral observations of *Chrysobracteon* are notably scarce. Andersen (1978) studied tunneling of several species, and showed that adults of *B. argenteolum* dig prodigiously into sand, *B. velox* and *B. lapponicum* extensively but to a lesser extent, and *B. litorale* rarely. Andersen (1978) also conducted substrate preference tests on *B. argenteolum*, *B. lapponicum*, and *B. litorale*, finding that *B. argenteolum* prefers finer dry sand to coarser dry sand, and *B. litorale* dry silt to dry sand. This is more or less consistent with the natural substrates of these beetles.

Chrysobracteon adults are predacious: besides occasional reports of adults feeding upon various arthropods (Gersdorf 1937, my observations), I have noted, in the course of dissecting numerous specimens of most *Chrysobracteon* species, recta filled with pieces of arthropod cuticle. The full course of their diet is unkown.

Chrysobracteon adults are generally active during the day, especially under bright summer sunshine, but they are at least occasionally nocturnal (against Larochelle (1975)). On the shores of the North Saskatchewan River at Deer Creek Bridge in Saskatchewan, a large number (123) of adults were collected between 2130 and 2230, 0.5 to 1.5 hours after sunset on a warm, moonless, September night. The adults were active on the surface, and several were feeding on dead insects, including nematocerous flies. A similar observation was made at the same locality on a cool, July night. That this is a general phenomenon has yet to be demonstrated.

Chrysobracteon overwinter as adults, and breed in the late spring and early summer. There are three larval instars, and pupation presumably occurs in mid to late summer. Teneral adults appear in the late summer and fall.

I have observed adults of all eleven North American species in flight; among strictly Palearctic species, members of *B. argenteolum*, *B. velox*, and *B. litorale* have been observed flying (Lindroth 1945). On warm, sunny days they are very active fliers, and will take to the wing quickly if approached, rather as do *Cicindela* adults.

3.8.6 Character states of *Chrysobracteon*

Variation in many characters was seen within *Chrysobracteon*. Some of this variety was useful in delimiting species, some for reconstructing phylogeny; some appeared useful for neither. In this section I introduce some of the character systems studied, describe some of the variation observed, and include tips for examination. If, during the course of using this paper, some question arises concerning a character that cannot be answered by the cited figures or descriptions, this section should be consulted.

I also comment briefly on characters that may prove valuable in future research, but which I have only superficially examined.

Color

The metallic hues of the body of *Chrysobracteon* specimens as seen under diffuse light are relatively distinct, and need no introduction. I rarely use them in formulating my systematic conclusions, in good part because of the large amount of within-taxon variation. I include them for the slight value they have in aiding identification of some species.

Appendage color is less variable within species, but it can be more difficult to determine the color of an appendage as it would be in its pristine state, because of grease darkening the paler regions of the appendage. Specimens to be examined should be as clean as possible.

Microsculpture

The most striking features of the microsculpture of a *Chrysobracteon* are silver spots on elytra of all species, and mirrors on elytra of some. These features are clearly studied under diffuse light on clean specimens.

Distinct silver spots are only found around discal setae ed3 and ed5 of the elytra, although indistinct silvery spots are present on the pronota of specimens of *B. inaequale* and some other related species. The number of silver spots, while generally two per elytron, varies to a considerable extent in some populations of *Chrysobracteon*. For example, in a series of 94 specimens of *B. lapponicum* from Old Crow River, northern Yukon territory, Canada (DRMa, UASM), 36 (or 19.1%) of the 188 elytra had three setiferous silver spots; four had one silver spot, one had four silver spots, while the remaining 147 elytra had two silver spots.

The difference visible between silver spots, mirrors, and other portions is often due to differences in the metallic hue of these regions, in addition to the depth of the microsculpture lines. As well, silver spots are depressed within the elytra, and mirrors are generally raised, further enhancing the distinctiveness of each region. For example, the depressed silver spots of *B. zephyrum* are silvery-grey or blue-green, the raised mirrors generally dark coppery red or purplish, and the surrounding elytral surface has a green or blue-green reflection. On their own, the microsculpture differences are not always striking (see, for example, the scanning electron micrograph of Fig. 61). In some species, especially shiny *B. semenovi*, *B. punctatostriatum*, and *B. stenoderum*, the mirrors and silver spots are not nearly so distinctive, because of the general reduction of microsculpture on these animals. The extent of mirrors on these beetles can best be observed in the more deeply microsculptured females.

Some species (especially *B. argenteolum*, *B. alaskense*, *B. carinula*, and *B. punctatostriatum*) exhibit a great variation in overall microsculpture depth, with specimens ranging from shiny to dull. As a result, the absolute depth of microsculpture of mirrors and silver spots varies from specimen to specimen, so that some individuals may have shiny mirrors (or silver spots), while others have quite dull mirrors (or silver spots). Thus, mirrors and silver spots must be defined by *relative* microsculpture depth, not absolute depth; the pattern within an elytron of relative microsculpture depth is more or less constant within a species.

Some generally shiny specimens, lacking areas that would be deemed mirrors on the basis of markedly shallower microsculpture, nonetheless have central patches of a distinct metallic color in regions that would typically contain microsculpture mirrors. I treat these color patches as mirrors. For example, while the shiny elytra of the *B. semenovi* holotype lack distinctly shinier patches, intervals 3 to 5 are darker, having a coppery tint lacking on the outer intervals; I consider this tint to delimit faint mirrors.

The extent and distribution of mirrors provide some of the best characters for species delimitation and identification. When present, mirrors occur on interval 3, surrounding the silver spots. There may also be mirrors on intervals 1 through 5 near the center of the elytra, as well as on the anterior portions of the same intervals, or the posterior portions of intervals 6 and 7. In general, mirrors on intervals 3, 5, and 7 are more prominent than those on other intervals. Figs. 7 to 23 illustrate some of the variation in mirror extent and position.

Sensilla

I investigated only a few sensillar characters, all setal.

One such character is suborbital setation. The head laterally beneath the eyes is either barren of setae (for example, in *B. punctatostriatum*, Fig. 60), or has a number of setae, ranging from relatively dense and long (*B. lapponicum* and others, Fig. 59), to shorter and sparser. The distinction between these states in not clear-cut, and as I have not quantified states, this character is relatively prone to errors in interpretation.

Protarsomere 4 of both sexes of most species of *Bembidion* possess ventrally an apical set of four setae, the two inner of which are thin, almost transparent, dorsoventrally flattened, and laterally expanded (Fig. 96a).

The bases of these setae are generally close-set, almost touching in the midline. However, three *Chrysobracteon* species have relatively cylindrical setae, with one of these species, *B. alaskense*, having their bases widely separated (Fig. 92).

During my study, several sensillar characters revealed themselves as being distributed in useful patterns within *Bembidion*, and these could be profitably studied in the future: number of setae on the anterior margin of the labial palpomere 2; number of submental setae; tarsomere 5 setation; profemur setation; metafemur setation.

Head

There is a wealth of mouthpart characters showing variation within *Chrysobracteon*, but I have been able to examine only a few of them. Mandibles vary in overall shape, in microsculpture (especially of the terebral/premolar region (Figs. 32-34)), in distinctiveness of premolars (compare Figs. 32 and 33), and in size of pores dorsally and mesally near the dorsal condyle (Figs. 35-36). My preliminary study of these characters revealed infraspecific variation within most of them, and I did not pursue them. Laciniae vary in width from narrow (Fig. 46) to robust and wide (Fig. 48). The shape varies in addition to simple width: some specimens have more definitely curved apices, or subapical indentations (Figs. 43, 44), or subapical ridges (Fig. 44); these characters warrant further study.

The shape of the mentum tooth has been used by Netolitzky (1942) and others as a character for *Chrysobracteon* taxonomy. Netolitzky (1927,1942:33-34) cautions against overestimation of the value of the mentum tooth as a systematic character; however, he does use it to separate his "subgenera" *Litoreobracteon*, *Argyrobracteon*, *etc*. Lindroth (1962:1) disagrees with this use, claiming that the mentum tooth is too infraspecifically variable: "for instance, the two male paratypes of *carrianum* Csy. (=*levettei* Csy.), both from St. Albert, Alberta, and with identical penis, have a quite different mentum tooth, triangular in one, practically parallel-sided in the other specimen". While there is some variation in shape of the mentum tooth within *Chrysobracteon* species, the variation I have seen is slight, and I consider it a stable enough character to be taxonomically useful. Even within *B. levettei* the mentum tooth is constant. I have examined the two paratypes of *B. carrianum* (USNM!) mentioned by Lindroth, and found them both to have the bulbous, parallel-sided mentum teeth characteristic of other members of that species. Figs. 49-56 illustrate some of mentum tooth shapes found in *Chrysobracteon*.

Elytra

A few elytral characters not carefully studied herein but which should be investigated are: interval 3 width; anterior protrusion of humerus (protruding in *B. punctatostriatum*, *B. inaequale*, and to a lesser extent in some other taxa).

Metathoracic wings

Two wing characters of potential future use are: pigmentation of metathoracic wing veins; shape of plica vein, whether sharply or gently curved.

Legs

Both sexes of many bembidiines and trechines have ventrally on protarsomere 4 an apical projection bearing four setae; the length of this projection varies between species, and is essentially absent in *B. alaskense*, *B. argenteolum*, and *B. punctatostriatum*. Under a light microscope, however, the length of such a projection can be difficult to determine accurately, and because of this I do not weight this character heavily in my analysis.

Claw shape, male protarsomere 1 and 2 shape, and protibial apices also show between-species variation, but I have not studied these in great detail.

Male genitalia

Because of the importance of male genitalia as a source of characters for species identification and phylogenetic analysis, I will describe their complicated structure in some detail.

Chrysobracteon aedeagi at rest consist of a sclerotized outer tube and a membranous internal sac, containing several sclerites, folded in inverted position within the tube (Fig. 99). The internal sac is attached to the tube dorsally near the apex, at the **ostium** (Lindroth, 1957b); this is the entrance into the internal sac from the exterior. During copulation the internal sac everts through the ostium; everted sacs are shown in Figs. 101 to 103. I will first describe the internal sac as it sits in rested, inverted position, beginning at the ostium. Many of the features are illustrated in Figs. 99 to 102.

At the ostium the left and right external walls of the aedeagus extend inward. The ostial cavity formed by these two walls is bounded anteriorly where they join (Fig. 99, "anterior edge of ostial cavity"). The natures of the microtrichia and scales in the "ostial microtrichal patch" associated with this edge provide good characters for species identification. These microtrichia or scales occasionally extend upward, forming a **dorsal field** on the outer wall of the aedeagus. The walls of the ostial cavity are membranous anteriorly and posteriorly, but centrally they are sclerotized in a roughly triangular patch called the **ostial flag** (Lindroth 1940).

A pathway into the internal sac is shown by the arrow in Fig. 99. The ostial cavity ends ventrally as the two enclosing membranes fold together to the right and continue on the right side of the cavity upward to near the dorsal surface; anteriorly they extend upward to the **dorsal plate**. Nearer the ostium, they are folded again to the right, and extend back down toward the venter. This simple pattern is complicated in some species by additional folds or membranous lobes. Anteriorly, near the sclerite complexes, membrane structure is much more complex, and I have not yet resolved the folding pattern.

There are two sclerite complexes on the internal sac. The largest, and the one to which the sperm duct connects, is the **central sclerite complex** (CSC, Figs. 99-102). It is partly enclosed by the dorsal plate. The left lobe of the CSC consists of two closely adjacent domes, from the rightmost of which a flange is extended down and merged with the right lobe. The right lobe often has a bulge dorsally on its left side; as the ventral edge of this bulge is heavily sclerotized, a dark line or ridge is visible on the lobe in lateral view in some species. The lobe is often sculptured: *B. lapponicum* usually has triangular scales and longitudinal striations, *B. inaequale* has a rugose surface, whereas *B. balli* and *B. foveum* usually are quite smooth. However, there seems to be a great deal of intraspecific variation, and I have not used this character in my analysis. Similar variation is also seen in microsculpture present on the left CSC lobe.

Apically from these lobes a complicated grooved spike (**flagellum**) projects; it is often species-specific in form (Figs. 99-102, 109-110, 129-144). It is presumably the conductor of sperm, and may enter the spermathecal duct during copulation (Schuler 1960). As the flagellum is partly surrounded by a scaly **flagellar sheath**, it can be very difficult to see in inverted position. The flagellar sheath is most prominent among *Chrysobracteon* species in the *B. argenteolum*-subgroup, *B. stenoderum*, *B. hesperium*, *B. lorquinii*, and the *B. inaequale*-subgroup. In Figs. 112 to 128, I have emphasized the flagellum beyond its normal visibility, and present in Figs. 129 to 144 drawings of isolated CSC's including flagella. The flagella provide excellent characters for species identification in *Chrysobracteon* and other *Bembidion*; if all other identification aids fail, I recommend dissecting out a CSC and comparing the isolated flagellum with Figs. 129 to 144.

From the baso-dorsal portion of the flagellum a heavily sclerotized wrinkled structure (Lindroth's **"ribbon brush"**, **"brush sclerite"**, or "BW") arises and passes on the right side of the CSC down toward the venter, where it joins the **ventral sclerite patch** (VSP). This latter complex is quite varied within the subgenus, and is one of the most useful genitalic features for specimen identification. In *Chrysobracteon*, it consists of two basins, connected by a dorsal ridge; the posterior basin extends distally into a wrinkled sclerotized patch.

Everted internal sacs clearly show lobes and surface sculpture of the membrane. SEM views of the membranes reveal a surprising complexity and diversity of microsculpture, with striking within-specimen (Figs. 103-106) and between species variation. I have not had time to study lobes or microsculpture in detail, but they seem to me to be some of the most, if not the most, fruitful areas of future

Bembidion morphology.

Female genitalia

Female genitalia vary considerably from species to species, as well as within species. Some characters, such as length of stylomere 2, were seen to be fairly constant within all species except *B. zephyrum*. Many other characters, such as the number of dorsolateral ensiform setae, show little variation within some species but much variation within others.

Spermathecal shape is another example of the latter. While most aspects of spermathecal shape are quite varied within some species, there are consistent differences between some species. I figure the spermatheca of most species, as some useful information is contained therein. Spermathecal shape will prove more useful in other subgenera and for studies of subgeneric delimitation and relationships.

Characters that have interesting patterns of variation, and which might prove useful in future research, include the form of sternum VIII, shape and setation of the valvifers (sternum IX), spermathecal duct coiling and turn pattern, and stylomere 1 structure. I have also not studied bursa copulatrix shape, although Erwin and Kavanaugh (1981) found it useful in their work on the *B. erasum* group.

Chromosomes

Chromosomes of all North American taxa of *Chrysobracteon* have been investigated; no Palaearctic species has been studied. Members of *Chrysobracteon* are relatively constant in chromosome number, although there is some variation. Autosomes differ little in length. The only striking variation in form is found in Y chromosomes: all species have a Y equal in size to the autosomes, or only slightly smaller, except *B. alaskense* and *B. carinula*, which have Y chromosomes less than two-thirds the length of the smallest autosomes. Karyotypes and other details of these species' chromosomes, as well as localities of capture of specimens examined, are presented elsewhere (Maddison 1985).

Larvae

The most obvious differences between first instar larvae of *Chrysobracteon* species are in color, especially of the head. Closer examination, however, reveals numerous other differences, mostly in sculpture and setation. This observation matches that of Goulet (1983) on elaphrine larvae, on which he found many systematically useful microsculptural and sensillar characters. In *Chrysobracteon*, variation among species was noted in microsculpture of the frontale, parietale, mandibles, and pronotum of first instars. The presence, length, and form of setae of the head capsule, thoracic nota, abdominal terga, and abdominal sternum IX also provided useful characters. For identification purposes, setal width and length are best characterized by comparison to nearby setae; thus I do not give absolute measurements. For example, I state that seta FR_3 of most *Chrysobracteon* is basally less than one-third the width of the nearby FR_2, but the absolute basal widths have not been measured.

Most larval character systems require no additional description, but some more comments about microsculpture are warranted. One of the few microsculptural characters I have investigated is frontal microsculpture. Most *Chrysobracteon* have a patch of microsculpture posteriorly and laterally on the frontale, in the position of the postero-lateral dark spots on Fig. 215. Descriptions of type of frontal microsculpture (whether or not multitoothed combs are present; character 60 of Table 2) are restricted to the anterior half of this patch, and characterization of extent of frontal microsculpture (character 59) applies only to the posterior half of the patch.

I have not carefully studied nasale structure; while there is much infraspecific variation, in good part due to wear, there are some differences between species. Urogomphus length varies between species, and is also worth further examination.

4. SPECIES OF *CHRYSOBRACTEON*

4.1 Species and subspecies recognition

4.1.1 Species concepts

I adopt a species concept similar to that of the evolutionary species concept of Simpson (1961:153) and Wiley (1978, 1981). The discussion that follows, while containing few if any novel ideas, serves to convey some of the systematic philosophy I used in treating *Chrysobracteon*.

Wiley (1981:25) defines an evolutionary species as "a single lineage of ancestor-descendent populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate". Wiley (1981:25) provides a definition of lineage: "one or a series of demes that share a common history of descent not shared by other demes". How much common history must be shared is not stated. It must be less than 100%, as no two demes share completely their history of descent, but it must be considerably more than 0%, as all demes within any monophyletic group share at least some history of descent. Wiley does not provide a definition of "identity", "evolutionary tendencies", or "historical fate", and the terms seem rather vague to me. Nonetheless, the gist of his definition seems reasonable to me; it simply needs a clearer formulation.

For dioecious organisms, a species, as I use the term, is a portion of a lineage of a phylogeny, and is composed of individual organisms. The starting and ending points of this portion are not easily decided. Wiley (1981:25) views species as arising at speciation events, and becoming extinct through lineage extinction or splitting. He writes that "ancestral species may become extinct during speciation events if they are subdivided in such a way that neither daughter species has the same fate and tendencies as the ancestral species", but it is not clear how one would know if the "fate" and "tendencies" have changed. Lineage-splitting events provide relatively distinct starting and ending points, and they may be the best such points in general, but I am by no means convinced of this. However, as the fossil record of *Chrysobracteon* is inadequate, consisting of only a few Miocene and Pleistocene fragments, I need not worry about this now, as I am essentially dealing only with the "thin veneer of the present". Among Recent organisms, then, a species consists of a time-transect of a lineage.

A lineage is itself not easily definable. Most biologists have an imprecise idea of a lineage as a set of organisms cohesively linked by breeding ties, which is distinct from other such sets. That is, it is a distinct portion of the genealogical nexus of life. But this is not a clear definition. A brief discussion of how one might formulate a rigorous definition may be worthwhile.

If one knew the pedigrees of all organisms (admittedly very unlikely, but imaginable), one could examine the genealogical nexus at a very high resolution, a resolution at which breeding relationships and ancestor-descendent relationships of individual organisms would be visible (Fig. 2a). As one steps back from this view, and observes the nexus at successively lower and lower resolutions, portions of the nexus would coalesce. Portions that coalesce first would be tightly interwoven portions along which traits of organisms could flow readily.

The eyes with which we would view the nexus, and which would direct its coalescence at low resolutions, would be genetic theory. Such theory would determine the amount of pedigree connectedness between organisms that would be important in the passage of traits along the phylogeny, traits whose evolution we are attempting to study. The lower the connectedness, the lower the resolution required before portions coalesce. Using genetic theory in choosing working units along and within which gene flow is high, and between which it is not, allows us to produce simple, explanatory theories about the diversity of forms possessed by those organisms. Details of a measure of connectedness determined by genetic theory to be important have yet to be worked out, and would probably vary from group to group in accordance with varying breeding systems.

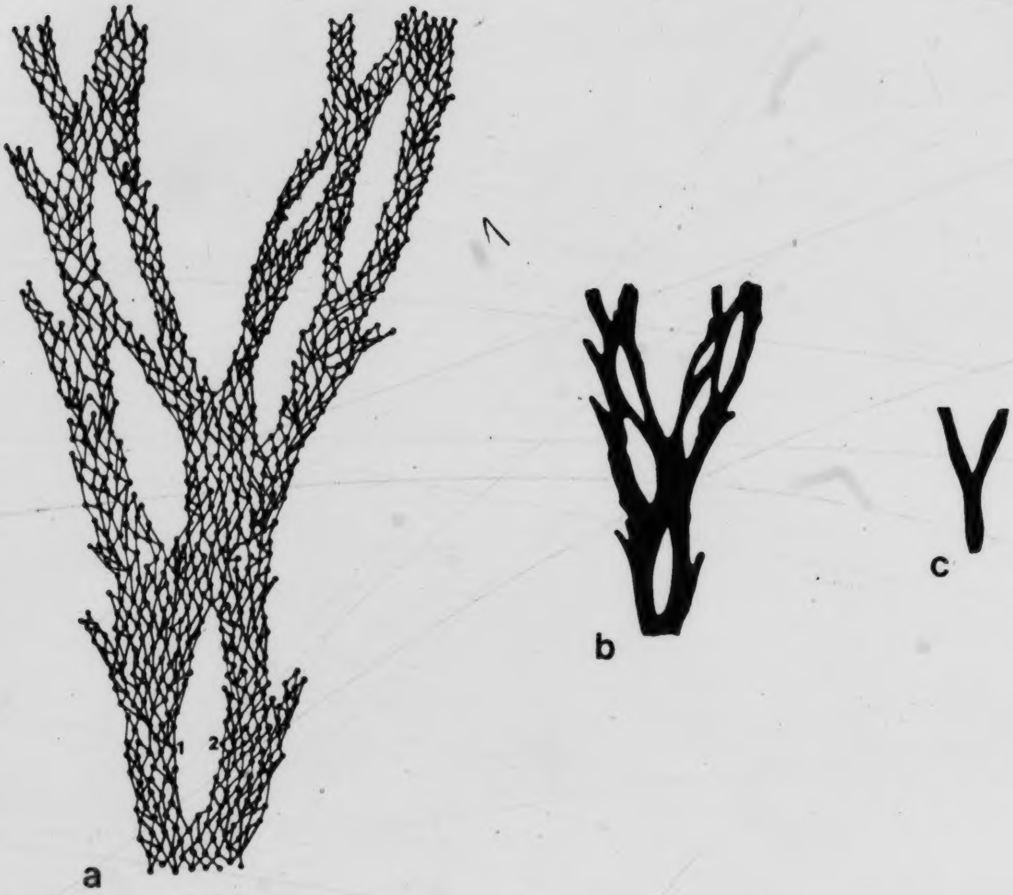
At a fairly low resolution, this nexus would appear like a braided watercourse, showing the vicariance and

Figure 2. A genealogical nexus at decreasing resolutions.

a. High resolution, showing breeding relationships between individual organisms.

b. Intermediate resolution, showing splitting and coalescence of populations.

c. Low resolution, showing lineages.



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subsequent rejoining of populations (Fig. 2b). Finally, at the lowest level of resolution (Fig. 2c), the nexus would appear as simple dichotomizing branches, with very little, if any, reticulation (at least in most animals). These branches would be lineages.

If one is working within one time horizon, as I am essentially doing with *Chrysobracteon*, then considerations not only of actual interbreeding relationships, but potential ones also come into play, as membership at one time-transect within a lineage is determined not only by past and present breeding ties, but future ones as well. The union of organisms 1 and 2 in Fig. 2a into one lineage in Fig. 2c is an example of this.

This view of a lineage, and of a species as a portion of such a lineage, may be fine *in theory*, but it is not directly applicable *in practice*. The entire pedigree of a group, such as that shown in Fig. 2a, is probably undiscoverable. As we cannot see the past and present breeding relationships directly, we have to infer them by the distribution of character states in available organisms. Species are recognized by a unique combination of character states possessed by their members, where this combination is distributed taxonomically, geographically, and ecologically in such a way as to indicate that extensive gene flow with other such groups is not now taking place, nor will it likely take place in the future.

Lineages (and thus species as I use the term) are genealogical, and thus some of the same sorts of evidence can be used for delimiting them as for subsequent inferences regarding their interrelationships – but here the pattern being sought is not one of sets of dichotomizing lineages (=low resolution pedigrees), but of anastomosing lines (=high resolution pedigrees of organisms). Species should not simply be the smallest collections of individuals possessing autapomorphies, as Rosen (1979) and others would suggest. I thus strongly disagree with Rosen's (1979:277) claim that "reproductive compatibility is a primitive attribute for the members of a lineage and has, therefore, no power to specify relationship within a genealogical framework". Reproductive compatibility *is* symplesiomorphic, I agree, but as genealogy consists of anastomosing lineages in addition to dichotomizing ones, compatibility is something necessary to consider if we wish to fully understand evolution.

We detect anastomosing lines by two methods: by detecting discordant apomorphies indicating past joining of two once-independent lines (Wanntorp 1983, Nelson 1983), or by more-direct evidence of reproductive cohesion. Within one small monophyletic group, one kind of "more-direct evidence" might be repeated discovery of one sort of male microsympatrically with just one sort of female, in addition to some observed matings between the types. If we ignored the reproductive compatibility indicated by such evidence, then we might produce numerous unusual (and unrealistic) reconstructed phylogenies. Highly ornamented males of several lineages might be collected together in one taxon, and their females with derived genitalia in another (W.P. Maddison pers. comm.).

Similarly, we detect lack of anastomosis between two forms by maintenance of distinctiveness in the face of sympatry. If in the area of sympatry there is a lack of the phenotypes expected if there were gene flow between the forms, then gene flow is probably absent or minimal, and the forms are maintaining their genealogical distinction. The traits studied in such comparisons need not be apomorphies; plesiomorphies would do just as well.

While ignoring anastomosis may satisfy a pattern cladist, I am a phylogeneticist, not a pattern cladist (for a discussion of the distinction, see Beatty (1982)). I am not willing to discard as myth all of current evolutionary theory. I believe that lineages (in the sense of low-resolution pedigrees) have existed and do exist, that they have split and evolved, that they are the "vehicles" of evolution, and that we can learn something about them. If we are to explain the origin of diversity of form, an enterprise I think is possible and fruitful, then we must use the "vehicles" of evolution – lineages – in our theories, if our theories are to be both explanatory and simple. If two lineages, separated for a time during which they developed autapomorphies and gave rise to daughter species, later merge to one, we should not ignore the reticulate aspect of the genealogy and force the pattern to be hierarchical. This same point is echoed by Wanntorp (1983). The avowed aims of systematics are the understanding of organic diversity, not "to reconstruct the genealogical history of lineages by a process of estimating a hierarchy of relationships" (Rosen 1979:277). Nature is not completely hierarchical; the reticulation within lineages (which serves in part to define them) and between lineages must be recognized and incorporated into our theories if we are to explain the variety of life.

In summary, a species, as a time transect of a lineage, can be recognized as a set of individual organisms possessing a unique combination of (ancestral or derived) character states. The character states might be structural, behavioral, geographic, or ecologic, *etc.*. Additional evidence may be provided in the form of directly observed matings between members of the set. I will expand on the practical means I used to delimit species in the next section, giving examples from *Chrysobracteon*.

4.1.2 Species delimitation within *Chrysobracteon*

I will not fully present my reasoning for my recognition of 17 species within *Chrysobracteon*. Any two forms each with their own unique character combination, occuring sympatrically, are judged to be separate species. Suffice it to say that 17 forms maintain their distinctiveness where they occur sympatrically (Table 1). Geographically separated forms that show intermediate regions of intermediate specimens are considered as belonging to one species (eastern and western forms of *B. inaequale* are the clearest examples of this). Other parapatric or allopatric forms are judged on the basis of similarity. If the forms are very similar, only consistently differing in one or a few characters, I have recognized them as belonging to the same species (for example, *B. levettei levettei* and *B. levettei carrianum* Casey, the Lake Baikal and Alaskan *B. alaskense*, southern Nearctic and northern *B. lapponicum*). If, however, the forms differ by at least the same magnitude as do sympatric species, they are construed as distinct species (for example, *B. litorale* and *B. levettei*, *B. velox* and *B. carinula*). This judgement is admittedly rather subjective; if any errors have been made, they are probably more errors in lumping than errors in splitting.

The mental analysis (presented later in the chapter "Phylogeny of *Chrysobracteon*") indicated the monophyly of 10 of the 17 *Chrysobracteon* species: *B. foveum*, *B. alaskense*, *B. semenovi*, *B. stenoderum*, *B. carinula*, *B. lapponicum*, *B. punctatostriatum*, *B. hesperium*, *B. zephyrum*, and *B. inaequale*; the phylesis of the other seven species was not apparent. Note, however, that paraphyly or polyphyly of most species could not be detected by the methods I used (in order to do that, I would have needed to treat each specimen

Table 1. Sympatry in *Chrysobracteon.*

Species abbreviations: **bl**: *B. balli*, **fo**: *B. foveum*, **ar**: *B. argenteolum*, **al**: *B. alaskense*, **sm**: *B. semenovi*, **st**: *B. stenoderum*, **ca**: *B. carinula*, **vx**: *B. velox*, **lp**: *B. lapponicum*, **pn**: *B. punctatostriatum*, **hs**: *B. hesperium*, **lq**: *B. lorquinii*, **ze**: *B. zephyrum*, **lvl**: *B. levettei levettei*, **lvc**: *B. levettei carrianum*, **ini**: *B. inaequale inaequale*, **ino**: *B. inaequale opaciceps*, **lt**: *B. litorale*, **bk**: *B. baikaloussuricum*.

S - species found sympatrically but not known to occur at exact same locality. **M** - species found microsympatrically, together on the same beach.

Species	**bl**	**fo**	**ar**	**al**	**sm**	**st**	**ca**	**vx**	**lp**	**pn**	**hs**	**lq**	**ze**	**lvl**	**lvc**	**in**	**lt**	**bk**
B. balli	-																	
B. foveum	M	-																
B. argenteolum	.	S	-															
B. alaskense	.	S	.	-														
B. semenovi	.	.	.	.	-													
B. stenoderum	.	.	.	.	.	-												
B. carinula	M	M	.	.	.	.	-											
B. velox	.	M	M	.	.	.	.	-										
B. lapponicum	M	M	M	M	.	.	M	.	-									
B. punctatostriatum	M	M	.	.	.	.	M	.	M	-								
B. hesperium	.	.	.	.	.	.	.	.	S	S	-							
B. lorquinii	.	.	.	.	.	.	.	.	S	S	M	-						
B. zephyrum	.	.	.	.	.	.	.	.	S	S	S	S	-					
B. levettei levettei	.	.	.	.	.	.	.	.	S	M	S	S	.	-				
B. levettei carrianum	M	M	.	M	.	.	M	.	M	M	.	.	.	.	-			
B. inaequale	M	M	.	S	.	.	M	.	M	M	M	M	S	M	M	-		
B. litorale	.	M	M	.	.	.	.	M	M	.	.	.	.	.	.	.	-	
B. baikaloussuricum	.	M	S	S	.	S	.	.	S	.	.	.	.	.	.	.	M	-

individually, a huge task!).

One species which may be shown to be paraphyletic is *B. levettei*; I could not demonstrate that *B. levettei levettei* plus *B. levettei carrianum* constitute a monophyletic group. If future work shows *B. levettei* to be paraphyletic, and collections from the Alberta foothills indicate a lack of recent gene flow between the montane *B. levettei levettei* and the lowland *B. levettei carrianum*, then I would favor splitting of the taxon into two separate species. However, in the face of ignorance, I prefer to follow Lindroth (1963), and retain montane and lowland specimens within one species.

4.1.3 Subspecies concepts

Subspecies, in contrast to species, are more phenetic units, although some genealogical component is present in their definitions. A subspecies is a phenetically distinct and geographically cohesive portion of a species, that is not connected to other such units by extensive geographic clines (such clines, if they do exist, are short and steep). Subspecies are units of convenience, recognized because they are worthy of discussion in comparative work. As such, they are less rigorously defined, and are somewhat more subjective. I recognize subspecies in only one *Chrysobracteon* (*B. levettei*), although further work may reveal the value of similarly dividing at least *B. alaskense*, *B. lapponicum*, and *B. inaequale*.

4.2 Checklist of extant *Chrysobracteon* taxa

- *B. balli* Lindroth
- *B. foveum* Motschulsky
- *B. argenteolum* Ahrens
- *B. alaskense* Lindroth
- *B. semenovi* Lindroth
- *B. stenoderum* Bates
- *B. carinula* Chaudoir
- *B. velox* (Linné)
- *B. lapponicum* Zetterstedt
- *B. punctatostriatum* Say
- *B. hesperium* Casey
- *B. lorquinii* Chaudoir
- *B. zephyrum* Fall
- *B. levettei* Casey
    - *B. levettei levettei* Casey
    - *B. levettei carrianum* Casey
- *B. inaequale* Say
- *B. litorale* (Olivier)
- *B. baikaloussuricum* Netolitzky

4.3 Identification of *Chrysobracteon* species

Keys are provided below for the identification to species of adults of *Chrysobracteon*, and known first instar larvae of the *Odontium* subgeneric group. Additional information useful for identification is provided in the account of each species. The figures (especially of habitus (Figs. 5-23) and male genitalia (Figs. 112-128)) may prove especially helpful.

4.3.1 Key to members of species of *Chrysobracteon*

Adults

1. Distinct smooth patches ("mirrors") on elytra, at least on interval 3 surrounding silver spots, or elytra generally smooth and shiny (Figs. 7 to 23).3

1'. Distinct elytral mirrors lacking, interval 3 between silver spots dull (Figs. 5 and 6).........2

2(1'). Pronotum small in comparison to the long elytra (El/Pwm = 2.44-2.60). Male protarsomere 1 relatively large (Fig. 76)........................ ....*B. foveum* Motschulsky, p. 101

2'. Pronotum and elytra of typical proportions (El/Pwm = 2.25-2.35). Male protarsomere 1 of normal size (Fig. 75).................*B. balli* Lindroth, p. 97

3(1). Intervals 6 or 7 with mirrors as or nearly as distinct as interval 3 mirrors, at or near level of silver spots (Figs. 17-23).......................13

3'. Outer elytral intervals lacking distinct mirrors, more or less uniform in luster....................4

4(3'). Midlateral seta of pronotum present (if the seta has broken off accidently, then its former presence is indicated by a pore puncture in the lateral margin)..5

4'. Midlateral seta of pronotum absent................8

5(4). Large (SBL generally more than 6.2mm) and shiny, with wide body (Fig. 11). Prothorax wide at base, with sides little sinuate. Mentum tooth large, bulbous, rectangular, without distinct epilobes (Fig. 52).. ....*B. punctatostriatum* Say, p. 132

5'. Smaller (SBL generally less than 6.2mm) and in most specimens duller. Body proportions more normal, not atypically wide (Figs. 12-14). Prothorax more constricted near base. Mentum tooth smaller, flatter, triangular or trapezoidal, epilobes distinct (Fig. 7).................................6

6(5'). Pronotum with distinct, long carina inside hind angles near base; carina extended to basal edge of pronotum (Figs. 12, 70)........................... ....*B. carinula* Chaudoir, p. 119

6'. Basilateral carina, if present, thin, oblique, and short, not extended to basal edge of pronotum.....7

7(6'). Elytral interval 3 wide, 1.7-2.6 times as wide as 2. Pronotum flatter, with flaring hind angles. (Holarctic.)....................................

..................*B. lapponicum* Zetterstedt, p. 127

7'. Elytral interval 3 narrower, 1.4-1.6 times as wide as second. Pronotum more convex, hind angles less prominent. (Palearctic.)..............................
..........................*B. velox* (Linné), p. 124

8(4'). Small (SBL = 4.4-5.4mm) specimen, elytra narrowing apically, interneurs deeply impressed; legs mostly pale, rufous. Generally with two setae in neighborhood of ed7. (Japan and neighboring mainland.).............*B. stenoderum* Bates, p. 117

8'. Generally larger, with wider elytra and less fusiform shape. Generally with one seta at ed7....9

9(8'). Shoulder margin longer (as in Figs. 68, 70-71), reaching or nearly reaching interneur 5. Aedeagi as in Figs. 114-115; female S2's exceptionally long (Figs. 150-151). (Palearctic region and Alaska.)
....10

9'. Shoulder margin shorter (as in Fig. 69), reaching at most just beyond interneur 6. Aedeagi as in Figs. 121-122; female S2's of normal length (Figs. 157-158). (Western North America south of Alaska.)
....12

10(9). Legs pale rufous. Dorsal surface of body shiny, with inconspicuous mirrors and silver spots. Interval 3 narrow (Fig. 9).........................
.......................*B. semenovi* Lindroth, p. 115

10'. Legs darker, at least apex of femur as well as tibia and tarsus infuscated. Duller, with mirrors and silver spots in most specimens more distinct. Interval 3 wider (Figs. 7 and 8)................11

11(10'). Duller, elytra in most specimens distinctly duller than pronotum. ed3 and ed5 near center of silver spots. Extra setae between eo4 and eo5 generally absent. Protarsomere 4 ventroapical setae widely separated (Fig. 92)..............................
.....................*B. alaskense* Lindroth, p. 109

11'. Dorsal surface, including elytra, shinier. ed3 and ed5 at or near anterior edge of silver spots. Extra setae between eo4 and eo5 generally present. Protarsomere 4 ventroapical setae narrowly separated (Fig. 93)..............................
.....................*B. argenteolum* Ahrens, p. 106

12(9'). Small (SBL = 4.7-5.8mm). Very shiny and dark. Microsculpture in shinier areas of elytral disc consisting of transversly stretched sculpticells, at least in males. Femora generally with basal half rufous..................*B. hesperium* Casey, p. 136

12'. Larger (SBL = 5.3-6.8mm). Duller and brighter. Elytral microsculpture isodiametric throughout. Femora entirely piceous or black..................
.....................*B. lorquinii* Chaudoir, p. 139

13(3). Mentum tooth rectangular, bulbous, epilobes indistinct. (Nearctic.) 14

13'. Mentum tooth flatten, not bulbous, epilobes distinct.......................................15

14(13). Mirrors on intervals 6 and 7 more or less isolated from mirrors on inner intervals, and present near level of posterior silver spot (Figs. 22-23)...................................*B. inaequale* Say, p. 155

14'. Outer elytral mirrors broadly connected to inner mirrors; outer mirrors closer to anterior silver spots. (Figs. 20-21)...*B. levettei* Casey, p.150

15(13'). Lateral margins of pronotum wide, flared into protrudent front angles (Fig. 19). (Pacific coastal beaches of North America.) ....*B. zephyrum* Fall, p. 143

15'. Pronotal margins narrower (Figs. 17-18). (Palearctic.) 16

16(15'). Pronotum flatter with sides little sinuate; midlateral seta absent; ed3 and ed5 generally at anterior edge of silver spots.....................................*B. baikaloussuricum* Netolitzky, p. 164

16'. Pronotum more convex, sides more rounded; midlateral seta present or absent; ed3 and ed5 generally closer to center of silver spots...............................*B. litorale* (Olivier), p. 160

First instar larvae

See key to larval instars, p. 55. In the following key I have included first instar larvae of all eleven North American *Chrysobracteon* species; I have omitted *B. argenteolum* and *B. litorale*, the larvae of which were described by Andersen (1966), as I have not seen specimens. I have also incorporated all other known larvae of the *Odontium* subgeneric-group, as these cannot yet be separated as a group from those of *Chrysobracteon*.

1. Parietale each with 2-6 large, tooth-like egg bursters in a cluster on each side near coronal suture (Figs. 228, 234); setae PR_{13}, ME_{14}, TE_{11} short (Fig. 250)..*B. carinula* Chaudoir, p. 119

1'. Parietale each with more numerous, smaller denticles (Figs. 226-227, 229-233, 235); if egg bursters large, then not set in a small cluster; setae PR_{13}, ME_{14}, TE_{11} relatively long (Figs. 240, 248)..2

2(1'). Setae ME_2 and TE_6 small (Figs. 246, 254)..........3

2'. Setae ME_2 and TE_6 relatively long.................5

3(2). Head capsule dark; pronotum with faint traces of microsculpture; seta PR_{10} present and long.............................*B. lapponicum* Zetterstedt, p. 127

3'. Head capsule pale with five dark spots; pronotum with distinct microtubercles; PR_{10} absent or small..4

4(3'). Seta EP_1 of abdominal segments 2-6 long, greater than one-third the length of EP_2; FR_3 thin, less than one-third the width of FR_2; PR_{10} present, short; setal groups gPR and gME absent; TEα absent; pronotum with microsculpture lacking between the two PR_{14}'s .... *B. (Ochthedromus) cheyennense* Casey

4'. Seta EP_1 very short, less than one-fifth length of EP_2; FR_3 thick, basally greater than one-half width of FR_2; PR_{10} absent, replaced by setal group gPR; gME and TEα present; pronotum with microsculpture present between the PR_{14}'s.. *B. punctatostriatum* Say, p. 132

5(2'). Small (head capsule width 275µm); head only slightly constricted posteriorly (Fig. 223), with long coronal suture (LCl/LHl = .196); frontale lacking microsculpture, with faint midlateral dark spots; parietale with large, widely separated egg bursters...................*B. (Odontium) aenulum* Hayward

5'. Larger (head capsule width 330µm or more); head more definitely constricted posteriorly (Figs. 210-217, 219-220), with shorter coronal suture (LCl/LHl ≤ .161); frontale generally with posterior-lateral microsculpture (lacking only in *B. alaskense*), with or without dark spots; parietale with smaller denticles.................6

6(5'). Frontale lacking microsculpture posteriorly, parietal microsculpture consisting of long, thin denticles (Figs. 227, 233); head capsule wide (LHw>490µm, LHw/LHl = 1.35-1.47)..*B. alaskense* Lindroth, p. 109

6'. Frontale with multipointed or singly pointed microsculpture, parietale with smaller denticles (Figs. 226, 231, 232); head capsule narrow (LHw<470µm, generally <420µm, LHw/LHl = .99-1.37).7

7(6'). Head capsule more or less uniformly dark..........8

7'. Head capsule mostly pale, or pale with three dark spots upon the frontale and generally one on each parietal side....................................9

8(7). Seta TE_{11} thin, blunt, parallel-sided; much narrower than TE_{10}...*B. foveum* Motschulsky, p. 101

8'. Seta TE_{11} tapered, about as thick basally as TE_{10}..............................*B. balli* Lindroth, p. 97

9(7'). Anterior two-thirds of posterior-lateral microsculpture patch of frontale consisting of relatively large, single denticles; nasale blunt (Fig. 193)......................................10

9'. Posterior-lateral microsculpture mostly multi-toothed combs; where single denticles, these are relatively small; nasale generally more sharply pointed (Fig. 192)..............................11

10(9). Microsculpture of parietale near coronal suture absent or very sparse.............................

........................*B. hesperium* Casey, p. 136

10'. Microsculpture of parietale near coronal suture more extensive and prominent........................ .*B. lorquinii* Chaudoir + *B. inaequale*-subgroup, pp. 139 to 156

11(9'). Pronotum with microsculpture (small tubercles) between PR_8, PR_9, and PR_{10}........................12

11'. Pronotum lacking microsculpture.................... ....*B. (Odontium) bowditchii* LeConte + *B. (O.) foraminosum* Sturm

12(11). Mandible long, markedly curved (Fig. 200).......... ....*B. (Odontium) coxendix* Say

12'. Mandible shorter, less curved (similar to mandible of Fig. 199)...................................... ....*B. (Odontium) confusum* Hayward

4.4 Accounts of species of *Chrysobracteon*

The arrangement of *Chrysobracteon* to follow matches that of the inferred phylogeny of the group, presented in the chapter "Phylogeny of *Chrysobracteon*" (p. 265). I include within *Chrysobracteon* two subgroups, the *B. argenteolum*-subgroup and the *B. inaequale*-subgroup, together containing eight of the 17 species. The other nine species are not arranged in subgroups.

4.4.1 *Bembidion balli* Lindroth

Bembidion balli Lindroth, 1962:15. HOLOTYPE male examined, in CNC, labeled: "McMurray, Alta. VIII.11.53 George E. Ball / Holotypus balli Lth. [red label, in Lindroth's handwriting] / HOLOTYPE CNC No 8375 [red label]". Type locality Fort McMurray, Alberta.

Derivation of specific epithet.– Patronym given by C.H. Lindroth to honor his friend and fellow carabidologist, George E. Ball.

Adult (Figs. 5, 35, 40, 49, 62, 68, 75, 96, 98, 99-102, 109, 112, 129, 147, 148, 165, 184, 186)

Diagnostic combination.– Body proportions as in Fig. 5; distinct elytral mirrors lacking; pronotum lacking long basilateral carina; male protarsomere 1 of normal size (Fig. 75); male aedeagus with flagellum long and ventrally curved (Fig. 129), apical boundaries of the two basins of the VSP well separated in left lateral view (Fig. 112).

Comparisons with related species.– Difficult to distinguish from specimens of *B. foveum*. *B. balli* members are smaller, with broader prothoraces and shorter, more convex elytra (compare Fig. 5 of *B. balli* with Fig. 6 of *B. foveum*). For *B. balli*, El/PWm = 2.25-2.35 (n=7); for *B. foveum*, El/PWm = 2.44-2.60 (n=9). *B. balli* generally more golden in color. Microsculpture of most specimens more deeply engraved, surface therefore duller, especially on forebody; microsculpture around anterior discal seta of elytron (ed3) irregularly disrupted in most specimens (Fig. 62), as opposed to the more smoothly circular pit in *B. foveum* (Fig. 63). In *B. foveum*, an extra seta is generally present on the elytra between eo4 and eo5, lacking in *B. balli*. Pores on surface of mandibles just mesal of dorsal condyle (Fig. 35) much narrower than those of *B. foveum* (Fig. 36); confirmed in four specimens of each species. As well, front angles of pronotum somewhat less protruded in *B. balli*, and humeral margin generally longer and more angulate. Males of *B. balli* can be distinguished by the considerably smaller basal protarsomeres (Fig. 75). Most external characters require experience to interpret, and, until this is gained, I recommend examination of the male aedeagus for more certain identification. Aedeagus thinner, less curved than in *B. foveum*, with narrower apex; right lobe of CSC generally less protruded in *B. balli*; apical boundaries of the two basins of the ventral sclerite patch of *B. balli* more widely separated in left lateral view; flagellum much longer, thinner, more curved in *B. balli*.

B. balli are occasionally confused with dark, unmetallic specimens of *B. carinula* lacking distinct mirrors (apparently through wear); however, *B. balli* adults do not have a long basilateral carina confluent with the pronotal base.

Description.– Character states as in Table 2, plus: *Size.* SBL = 4.8-5.8mm. *Color.* Dorsal surface bronze or grey-bronze, silver spots blue, bronze, or aeneous. Appendages for the most part piceous, except for the venter of antennomere 1, the pro- and mesotrochanters, and the base and venters of femora, which are testaceous; antennomeres 2 through 4 and tibiae paler ventrally in some specimens. *Microsculpture.* Silver spots inconspicuous, not or only slightly depressed below rest of interval; elytra lacking mirrors, although interval 3 in some specimens slightly darker between silver spots, giving the illusion of very faint mirrors. *Thorax.* Sides of pronotum sinuate, greatest width at or slightly before middle. *Elytron.* Interneurs slightly to moderately impressed; interval 3 not or only slightly wider than 2. *Female genitalia.* Spermatheca as in Fig. 165, ramus lobe in many specimens longer; cornus long, slightly curved, dorso-basal bulb curved, short. No posterior lobe at base of spermathecal duct. Stylomeres as in Fig. 148.

First instar larva (Figs. 191, 196, 210, 240, 242, 245, 248, 252, 255, 257)

Diagnostic combination.– Head capsule dark (Fig. 210), with faint trace of three-spotted frontal pattern; parietale with slightly darker patch in front of PA_4 and PA_7; parietal denticles small; ME_2 and TE_6 long; TE_{11} tapered, basally thick, as thick as TE_{10} (Fig. 248); abdominal segment VIII with EP_1 less than one-half width of EP_2.

Comparisons with related species.– From the very similar *B. foveum*, distinguished by thick, tapered setae TE_{11} of the abdominal terga. As well, mandible of *B. balli* with only one or two denticles near seta MN_1, in contrast to the more numerous denticles of *B. foveum*; setae FR_1 and FR_3 shorter than those of *B. foveum*.

From the other *Bembidion* with dark larval head capsules, *B. lapponicum*, distinguished by many traits, including the smaller parietal denticles; narrow setae FR_1, FR_3, and segment VIII EP_1; long setae ME_2 and TE_6; absence of setae ST_2 on abdominal sternum IX.

Description.– As in Table 2, plus: *Size*. LHw = 400-415 µm, LHl = 360-380 µm, LCl/LHl = .132-.147. Four specimens measured.

Second instar larva (Fig. 258)

Description.– LHw= 540-595 µm (n=2). Frontale without extra setae near FR_3, and lacking microsculpture posteriorly. Head and pronotum with accessory microsetae clearly over three times longer than wide. Microsculpture absent centrally on pronotum. Urogomphus with seven long setae.

Specimens examined.– I have seen 259 adults, 29 first instars, and 5 second instars from the following collections: AMNH, BMNH, CAS, CNC, CUIC, DRMa, HNHM, ICCM, MCZ, SMNH, UASM, USNM, ZIL, ZMLS.

Geographic distribution.– Found only in west-central Saskatchewan and at the type locality of Fort McMurray, Alberta (Fig. 261). The report of *B. balli* from Churchill, Manitoba (Elias 1984), is based on a series of *B. carinula* adults (SAEl!).

Geographic variation.– None noted over the small known range.

Habitat.– Known only from rivers, on barren beaches composed mainly of sand.

Phylogenetic relationships.– With uncertainty, I place *B. balli* as the sister group of *B. foveum* (Fig. 278).

4.4.2 *Bembidion foveum* Motschulsky

Bembidium foveum Motschulsky, 1845:271. Keleinikova (1976:198) reports four SYNTYPES in ZMUM, but later in the same paper (p.223) she states that the collection contains one LECTOTYPE and one paralectotype. Types not examined. Type locality L. Baikal, U.S.S.R.

Bembicidium glabriusculum Motschulsky, 1845:272. One SYNTYPE (a holotype?) in ZMUM (Keleinikova 1976:199), not examined. Type locality Sitka, Alaska.

Bembidion bryanti Carr, 1932:191 (not *B. bryanti* Andrewes 1921:249). HOLOTYPE male examined, in CNC, labeled: "Norman, N.W.T. Sept.23.1929 Owen Bryant / Mackenzie River 1929 Trip. Lot Owen Bryant 23 / above San Sault Rapids 70 mi Norman [handwritten] / HOLOTYPE Bembidion bryanti Carr No 3435 [red label] / Holotype Bembidion bryanti Carr ex coll. F.S.Carr [red label] / SLIDE No. 2102 [green label] / Bembidion foveum Mtsch Det. Lindroth, 1961". Type locality Mackenzie River, 70 miles below Fort Norman, above Sans Sault Rapids.

Bembidion beringi Netolitzky, 1940:164 or 1942:54. HOLOTYPE male examined by Lindroth (1962), in Swedish Riksmuseum, Stockholm. Type locality Petropavlovsk, Kamchatka, USSR.

Bembidion grahami Hatch, 1951:114. HOLOTYPE male examined, in OSUO, labeled: "Findlay Forks B.C. 22/6 1930 Coll. R. Graham [partly handwritten] / Bembidion (Chrysobracteon) foveum Mots. M. Hatch 1969 / bryanti Carr (Prob = Siberian species) Det. Lindroth, 1958 / TYPE Bembidion (Chrysobracteon) grahami 1950 - M. Hatch [red label, handwritten]". Type locality Findlay Forks, British Columbia, Canada.

Derivation of specific epithet.– From the Latin *fovea*, meaning "pit", referring to the elytral silver spots.

Adult (Figs. 6, 24-27, 29-32, 36, 37-39, 41, 63, 69, 76, 113, 130, 149, 166, 183)

Diagnostic combination.– Body proportions as in Fig. 6; distinct elytral mirrors lacking; pronotum lacking long basilateral carina, with midlateral seta; male protarsomere 1 exceptionally large (Fig. 76); flagellum of male aedeagus relatively short and thick (Fig. 130); apical boundaries of two basins of VSP narrowly separated in left lateral view (Fig. 113).

Comparisons with related species.– Similar to *B. balli*; many specimens difficult to identify with certainty using external characters. For a discussion of differences between the species, see account of *B. balli*.

Description.– As in Table 2, plus: *Size*. SBL = 5.5-6.5mm. *Color*. Dorsal surface greyish, in many specimens with bronze or aeneous tint; silver spots bronze, greenish, or bluish. Appendages colored as in *B. balli* but slightly darker, pale areas a bit more rufous. *Microsculpture*. Disc of pronotum diffusely shinier. Elytral mirrors absent, although in some specimens the inner intervals are slightly shinier; silver spots in many specimens slightly more depressed into elytra than in *B. balli*. *Thorax*. Sides of pronotum sinuate; greatest width generally further forward than in *B. balli*, before middle. *Elytron*. Interneurs shallow to moderately impressed; interval 3 only slightly wider than

2. *Female genitalia*. Spermatheca as in Fig. 166, similar to that of *B. balli*. No posterior lobe at base of spermathecal duct. Stylomeres as in Fig. 149.

First instar larva (Figs. 199, 201-203, 205, 211, 226, 232, 238, 249)

Diagnostic combination.– Head capsule dark, with faint trace of three-spotted frontal pattern; parietal denticles small; ME_2 and TE_6 long; TE_{11} parallel-sided, bluntly tipped, basally thin, less than one-half width of TE_{10} (Fig. 249); abdominal segment VIII with EP_1 less than one-half width of EP_2.

Comparisons with related species.– Very similar to larva of *B. balli*; best distinguished by the thin, blunt, parallel-sided setae TE_{11} of the abdominal terga; a few more characters are mentioned under the account of *B. balli*.

From *B. lapponicum*, distinguished by the smaller parietal denticles; narrow setae FR_1, FR_3, TE_{11}, and segment VIII EP_1; long setae ME_2 and TE_6; absence of setae ST_2 on abdominal sternum IX.

Description.– As in Table 2, plus: *Size*.– LHw = 460-465 μm, LHl = 410-415 μm, LCl/LHl = .135-.146. Two specimens measured.

Specimens examined.– I have seen 645 adults and 17 first instars from the following collections: AMNH, BJCa, BMNH, CAS, CNC, CUIC, DHKa, DRMa, HNHM, ICCM, JKLi, MCZ, OSUO, ROM, SMNH, UASM, UBC, UMHF, USNM, ZMLS.

Geographic distribution.– A Holarctic species (Fig. 262). In the Palearctic, from northeasternmost Europe, across the width of northern Asia to Kamtchatka. In North America (Fig. 262b), from Alaska east to the Anderson River, and south to central Saskatchewan.

Geographic variation.– No variation correlated with geography was noted.

Habitat.– Found only on the banks of rivers, most commonly on barren, silt-mixed sand.

Phylogenetic relationships.– Apparently the sister species of *B. balli* (Fig. 278).

B. argenteolum-subgroup

This group is a taxonomically difficult complex of forms. I am treating it as three species (*B. argenteolum*, *B. alaskense*, and *B. semenovi*), as did Lindroth (1962, 1965), but I am not entirely satisfied with this arrangement. *B. semenovi* is probably a distinct species, although it is possible that the holotype is simply an aberrant *B. argenteolum*. The distinctiveness of *B. alaskense* from *B. argenteolum* is more doubtful. While European *B. argenteolum* are quite different from Alaskan *B. alaskense*, the few specimens I have from the Lake Baikal region are somewhat intermediate (they are nearly the size of European *B. argenteolum*, but otherwise match Alaskan

B. alaskense), suggesting that the distinct forms may simply be two extremes of one species. I discuss these specimens further under *B. alaskense*. However, the few specimens I have from the region in between Lake Baikal and Alaska are more typical *B. argenteolum*, indicating that the two forms are not simply ends of a cline. Because of this, and as the material before me from the eastern USSR is rather meager, I will not synonymize the two names; more specimens from eastern Asia are needed to settle the problem.

4.4.3 *Bembidion argenteolum* Ahrens

Bembidion Argenteolum Ahrens, 1812:23. TYPE material lost (see Lindroth (1962:11)). Type locality Halle, Germany.

Bembidium azureum Gebler, 1833:276.

Bembidium chalybaeum Sturm, 1843:36. *Nomen nudum*, as there is no description.

(*Bembidion argenteolum* v. *amethystinum* Meier, 1899:98. [Name unavailable as clearly intended to be infrasubspecific.])

Bembidion argenteolum var. *virens* Schilsky, 1908:604 (not Gyllenhal 1827:407). Types presumably in the Schilsky collection, Zool. Mus., Berlin (Horn and Kahle 1937). Type locality Posen (=Poznań), Poland. [Original description gives no indication that author intended the name to be infrasubspecific, and thus the name is available (ICZN Third edition Article 45(g)).]

Derivation of specific epithet.– From the Latin *argentum*, meaning silver, referring to the sparkling, metallic appearance of the elytral "silver spots".

Adult (Figs. 7, 77, 88, 93, 97, 114, 131, 150, 167)

Diagnostic combination.– Large (SBL = 5.4-7.0mm, generally over 5.8 mm); elytral mirrors on intervals 3 and 5, in some specimens on first five intervals, no distinct mirrors on intervals 6 or 7; pronotum lacking long basilateral carina, without midlateral seta; ventroapical setae of protarsomere 4 narrowly separated (Fig. 93); lateral projection on male protarsomere 3 lacking (Fig. 93).

Comparisons with related species.– Adults are very similar to those of *B. alaskense* and *B. semenovi*. Larger than *B. alaskense*, shinier, silver spots not on intervals 2 or 4. Setae ed3 and ed5 located at anterior margin of silver spots; most specimens with at least one seta between elytral setae eo4 and eo5. Ventroapical setae of protarsomere 4 narrowly separated. Aedeagus of *B. argenteolum* generally larger, straighter, with a less evident ventrolateral bulge than *B. alaskense*. The only consistent difference noted was in the CSC flagellum: that of *B. argenteolum* has a narrower base and a less-sinuous dorsal margin. Duller than *B. semenovi*, with wider interval 3, and without lateral projection on male protarsomere 3.

Distinguished from the sympatric *B. velox* and *B. lapponicum* by the lack of midlateral pronotal setae, larger size, and (in some specimens) more distinct mirrors of elytral intervals 4 and 5.

Description.– As in Table 2, plus: *Size.* SBL = 5.4-7.0mm. *Color.* Mirrors with dark brass, coppery-red, aeneous, or green reflection; rest of dorsal surface dark bronze, purple, or blue; mirrors of many specimens contrasted in color with rest of dorsal surface. Appendages mostly infuscated, piceous, with ventral portion of antennomere 1, venter at base of antennomeres 2 through 4, and base of femora rufous. *Microsculpture.* Pronotum with shiny disc. Elytron shinier than that of *B. alaskense*, about as shiny as pronotum. *Thorax.* Pronotum convex, with rounded margins. *Elytron.* Convex, humeral margin longer and more angulate than in many *B. alaskense*, nearly extended to interneur 5; interneurs slightly to moderately impressed; interval 3 distinctly wider than 2. *Female genitalia.* Spermatheca varied; cornu more or less curved in most specimens (Fig. 167). No posterior lobe at base of spermathecal duct. Stylomeres long, as in Fig. 150.

First instar larva

Description.– See Andersen (1966) for more details about all larval stages. He includes information about only a few of the first instar characters I have studied. Head pale, centrally darker. Judging from his figures 12-14, setae PR_{13}, ME_{15}, and TE_{11} are long, and PR_{10} is apparently present and long.

Specimens examined.— I have seen 126 adults from the following collections: BMNH, CAS, DRMa, HNHM, MCZ, UMHF, USNM, ZMLS.

Geographic distribution.— Isolated on Ireland; on the mainland from western France and northern Italy, to Scandinavia, and eastward to the Lena River and Ussur regions of the U.S.S.R. (Fig. 263; Netolitzky and Meyer 1933).

Geographic variation.— None noted over Europe and western Siberia. The one female I have examined from far eastern U.S.S.R. ("Ussuri", UMHF), is more deeply microsculptured than other specimens, but otherwise appears to be a normal *B. argenteolum*.

Habitat.— On barren or nearly barren sand banks of rivers or lakes (Lindroth 1945).

Phylogenetic relationships.— Most closely related to *B. alaskense* or *B. semenovi*.

4.4.4 *Bembidion alaskense* **Lindroth**

Bembidium conicolle Motschulsky, 1845:273. Two SYNTYPES in ZMUM (Keleinikova 1976:192). Type locality Hamar Daban Mountains, near Lake Baikal. **Tentative new synonymy.**

Bembicidium conicicolle Motschulsky, 1850:16; unjustified emendation of *Bembidium conicolle* Motschulsky, 1845.

Bembidion alaskense Lindroth, 1962:9. HOLOTYPE male examined, in CAS, labelled: "Grants Cabin, Toms Lake, Alask. Pen., Alask. VII-8-1919 [handwritten] / Van Dyke Collection / Holotypus alaskense Lth. [red label, partly in Lindroth's handwriting]". Type locality Lake Brooks (=Toms Lake [Orth 1967]), Alaska Peninsula, Alaska.

Bembidion colvillense Lindroth, 1965:126. HOLOTYPE male examined, in MCZ, labeled: "Umiat, Alaska Aug. 6, 1958 George E. Ball / MCZ Holotype 32753 [red label] / Holotypus colvillense Lindroth [red label, in Lindroth's handwriting]". Type locality Umiat, Alaska. **New synonymy.**

Notes about synonymy.— I have not yet examined the type material of *B. conicolle* Motschulsky. Lindroth (1962:11) tentatively considered *B. conicolle* to be a synonym of *B. argenteolum*. If he was correct that *B. conicolle* is a *B. argenteolum*-subgroup member, then it may well be a senior subjective synonym of *B. alaskense*, as the only *B. argenteolum*-subgroup members I have seen from three localities around the type locality of *B. conicolle* are *B. alaskense*. I take no nomenclatural action, and await study of the *B. conicolle* type material.

The type of *B. colvillense* Lindroth is more heavily microsculptured than most southern *B. alaskense*, with the mirror on interval 4 thereby fainter. While this mirror is fainter than those on intervals 3 and 5, it is still distinct, contrary to Lindroth's (1965) statement; the interneurs are also not particularly regular. In the *B. colvillense* holotype the unpigmented nature of the aedeagus makes interpretation of its structure difficult, but in visible aspects it appears identical to *B. alaskense*. A sample from the Killick River (AMor, UASM!), not far from the type locality of *B. colvillense*, contains specimens similar to the *B. colvillense* type, the *B. alaskense* type, and a range of intermediates. It thus seems clear that all specimens from the Colville and Killick rivers belong to *B. alaskense*.

Derivation of specific epithet.– From "Alaska", state of capture of the type series.

Adult (Frontispiece and Figs. 8, 47, 50, 92, 110, 115, 132, 146, 151, 168)

Diagnostic combination.– Small (SBL = 5.0-6.3 mm, Alaskan specimens 5.0-5.7 mm); elytral mirrors on intervals 3 and 5, in some specimens on intervals 3 through 5, no distinct mirrors on intervals 6 and 7; pronotum lacking long basilateral carina, without midlateral seta; ventroapical setae of protarsomere 4 widely separated (Fig. 92); lateral projection on male protarsomere 3 lacking.

Comparisons with related species.– Distinguished from *B. argenteolum* by smaller size, and generally darker appendages. Prothorax in most specimens with disc shiny, otherwise the microsculpture is stronger than most

B. argenteolum, and thus the surface is duller. Silver spots in many *B. alaskense* specimens larger, extended onto intervals 2 and 4. Seta of silver spot located nearer center of spot. Interval 9 of elytra generally lacking setae between eo4 and eo5. Ventroapical setae of protarsomere 4 widely separated. For genitalic differences, see comments under *B. argenteolum*.

From *B. lapponicum* and *B. carinula* distinct in lacking the midlateral pronotal seta, and more definite mirrors on interval 5 (and generally also 4).

Description.– As in Table 2, plus: *Size*. SBL = 5.0-6.3mm. *Color*. Darker than *B. argenteolum*. Dorsal surface dark copper, bronze, aeneous, or bluish, mirrors in many specimens slightly purplish or reddish. Appendages dark, piceous or black, except for the venter of the antennomere 1, the base of femora, and the pro- and mesotrochanters, which are rufous; tibiae slightly paler in a few specimens, as is the maxillary palpomere 2. *Thorax*. Pronotum narrower than *B. argenteolum*, sides straighter, not as rounded. *Elytron*. Humeral margin short to medium-long, extended to interneur 5 or not, generally not as angulate as in *B. argenteolum*; interneurs slightly to moderately impressed, in many specimens disrupted (especially 3 and 4); interval 3 wide, in many specimens abruptly widened just around silver spots. *Female genitalia*. Spermatheca (Fig. 168) as for *B. argenteolum*, cornu of varied shapes. Stylomeres as in Fig. 151.

First instar larva (Figs. 212, 227, 233, 236)

Diagnostic combination.– Head capsule wide, diffusely darker centrally, frontale without traces of spots (Fig. 212); parietal denticles large, thin (Figs. 227, 233); PR_{13}, ME_2, ME_{14}, TE_6, TE_{11} long; abdominal segment VIII with EP_1 less than one-half width of EP_2.

Comparisons with related species.– Distinguished from the other species with centrally dark head capsules, *B. carinula*, by the large setae ME_2 and TE_6, and the smaller, more widely distributed parietal denticles of *B. alaskense*.

Description.– As in Table 2, plus: *Size*. LHw = 490-500 µm, LHl = 340-365 µm, LCl/LHl = .110-.118. Three specimens measured. *Microsculpture*. Frontale without denticulate microsculpture (or at most with a few denticles around sensillum FRb). Parietale lacking microsculpture near coronal suture. Mandible with prominent denticles dorsally near MN_1. *Head* wide, LHw/LHl = 1.35-1.47 (n=3).

Second instar larva

Description.– LHw = 700-750 µm (n=2). Frontale with extra setae near FR_3, and lacking microsculpture posteriorly. Head and pronotum with accessory microsetae clearly over three times longer than wide. Microsculpture absent centrally on pronotum. Urogomphus with seven long setae.

Specimens examined.– I have seen 157 adults, 156 first instars, 23 second instars, and 27 third instars from the following collections: AMNH, AMor, BMNH, CAS, CNC, DRMa, HNHM, MCZ, OSUC, OSUO, UASM, USNM, ZIL, ZMLS.

Geographic distribution.– Known from Alaska, from the Alaska Peninsula in the south to the Brooks Range in the north (Fig. 264); also in the region of Lake Baikal (Fig. 263).

Geographic variation.– While there is much within-population variation in Alaska, southern specimens seem in general to be darker, shinier, and with shorter appendages than specimens from north of the Brooks Range. Genitalic variation appears uncorrelated with external variation or geography. Specimens from Lake Baikal are larger than Alaskan specimens (SBL = 5.4-6.3mm, mean=5.86mm, S.D.=.31, n=7 for Njurga Bay, Lake Baikal; SBL = 5.0-5.7mm, mean=5.33mm, S.D.=.26, n=10 for Lake Brooks, Alaska), but otherwise possess all of the distinguishing features of *B. alaskense*: widely separated ventroapical setae of protarsomere 4, sinuate flagella, *etc.*.

Habitat.– On the bank of Lake Brooks, Alaska, larvae and adults were abundant on a barren, dark, volcanic-sand beach. On the north slope of the Brooks Range in northern Alaska, specimens were found under flood debris on the barren sand-silt bank of the Killick River (A.V. Morgan pers. comm.), and on the mostly barren sand-clay bank of the Colville River (Lindroth 1962:126).

Phylogenetic relationships.— A member of the *B. argenteolum*-subgroup, but beyond that its relationships are unclear (Fig. 278).

4.4.5 *Bembidion semenovi* Lindroth

Bembidion semenovi Lindroth, 1965:127. HOLOTYPE male examined, in ZIL, labeled: "[handwritten label in Cyrillic, mostly indecipherable to me, ends in '8.VIII.910 A. Jacobson'] / Bracteon sp.n.? [hand-written] / B (Chrysobracteon) ?semenovi sp.nov. [hand-written] Kryzhanovskij det./ Holotypus semenovi Lth. [red label, partly in Lindroth's handwriting]". Type locality (Lindroth 1965:127): Black Irtysh R., near the mouth of the Kaldzhir R. (=Markakol' R.), approximately 140 km NNE Zaisan, Siberia.

Derivation of specific epithet.— Patronym given to honor the coleopterist, A. Semenov-Tian-Shanskij.

Adult (Figs. 9, 78)

Diagnostic combination.— Large (SBL = 6.1mm), convex, shiny; interval 3 narrow, with small silver spots (Fig. 9); appendages pale rufous or rufotestaceous; pronotum without long basilateral carina, without midlateral seta; male protarsomere 3 with lateral projection (Fig. 78).

Comparisons with related species.— Difficult to distinguish from some specimens of *B. argenteolum*. Shinier, with narrower interval 3, and smaller silver spots. Appendages paler than *B. argenteolum*, with antennomere 1 entirely rufotestaceous. Protarsomere 3 of male with lateral projection (Fig. 78). Male genitalia of the holotype is identical in all studied aspects to that of *B. argenteolum* specimens.

Description.– As in Table 2, plus: *Size*. SBL = 6.1mm. *Color*. Dorsal surface aeneous, mirrors with coppery tint. Appendages very pale, entirely rufotestaceous, although antennomeres 3 to 11 and tarsi slightly infuscated. *Microsculpture*. Disc of pronotum slightly shinier than in *B. argenteolum*. Elytra very shiny; mirrors on intervals 2 to 5, none on 6 or 7; mirrors only slightly shinier than the background; silver spots inconspicuous. *Thorax*. Pronotum shaped as in members of *B. argenteolum*, that is, convex with rounded sides. *Elytron* convex, humeral margin moderately long, almost extended to interneur 5; interneurs straight, moderately impressed; interval 3 narrow.

First instar larva

Unknown.

Specimens examined.– Only the holotype seen (ZIL).

Geographic distribution.– Known only from the type locality (Fig. 263).

Habitat.– Unknown.

Phylogenetic relationships.– Most closely related to *B. alaskense* and *B. argenteolum* (Fig. 278).

4.4.6 *Bembidion stenoderum* Bates

Bembidium stenoderum Bates 1873:300. TYPE, not examined, BMNH. Type locality Osaka, Japan.

Derivation of specific epithet.– From the Greek "*στενξσ*", meaning narrow, referring to the narrow body of members of this species.

Adult (Figs. 10, 116, 133, 152, 169)

Diagnostic combination.– Small and narrow, body fusiform (Fig. 10); surface shiny, with mirrors on intervals 3 through 5, and in most specimens with faint mirrors on intervals 6 and 7; ed3 and ed5 in large pit; prothorax sides little rounded, with wide base, and midlateral seta absent; humeral margin long, extended to interneur 5; interneurs deeply engraved; generally with two setae in ed7 area. Aedeagus slender, with straight basal portion and ventrally bent apex (Fig. 116); sclerite complexes far removed from basal orifice; right lobe of CSC ridged; ostial microtrichial patch very small.

Comparisons with related species.– The fusiform shape and other characters mentioned in the diagnosis are distinctive; specimens are not likely to be misidentified.

Description.– As in Table 2, plus: *Size*. SBL = 4.4-5.4mm. *Color*. Dorsal surface of body aeneous or bronze, mirrors purplish, silver spots bluish or aeneous. Appendages pale: most of antennomere 1 pale rufotestaceous, at least base of following three articles pale; legs infuscated at least at joints and on tarsi, slightly more generally infuscated in some examples. *Thorax*. Sides of pronotum little sinuate, base wide (greatest width of prothorax at hind angles); basal tubercle relatively flat. *Elytron* tapered toward apex; humeral margin long, extended to inside interneur 5; interneurs moderately to markedly impressed, more so than any other *Chrysobracteon* (even interneur 8 is more or less deepened throughout its length); interneur 3 abruptly deeper around silver spots. *Female genitalia*. Spermatheca varied, as in Fig. 169; although cornu in some specimens shorter and straighter. Spermathecal duct without posterior lobe. Stylomeres as in Fig. 152.

First instar larva

Unknown.

Specimens examined.– I have seen 44 adults from the following collections: BMNH, DRMa, HNHM, MCZ, UASM, USNM.

Geographic distribution.– Restricted to Japan and the neighboring mainland (Fig. 263).

Geographic variation.– None seen in the few specimens at hand, although the only female I have seen from "China" (BMNH) is larger than average and quite dull.

Habitat.– Not known to me.

Phylogenetic relationships.– I tentatively place this taxon as the sister group to the *B. argenteolum*-subgroup (Fig. 278).

4.4.7 *Bembidion carinula* Chaudoir

Bembidium carinula Chaudoir, 1868:239. LECTOTYPE male designated by Lindroth 1963:237, in MNP, not examined. Type locality "*la Terre de Rupert*", Rupert's Land, former name for the entire drainage basin of Hudson's Bay, thus including most of northern Quebec, Ontario, Manitoba, etc. (Lamb 1971); not Rupert House, Quebec, as stated by Lindroth (1963).

Bembidion tuberculatum Notman, 1929:157. HOLOTYPE female, examined by Lindroth (1962), in Staten Island Museum. Type locality Marquette, Michigan, U.S.A.

Derivation of specific epithet.– From the Latin "*carina*", meaning "keel" or "ridge", presumably referring to the prominent basilateral carina of pronota of adults.

Adult (Figs. 12, 70, 117, 134, 145, 154, 170, 185, 187, 188)

Diagnostic combination.– Pronotum with long, distinct basilateral carina extended to base (Fig. 12, 70), as well as a midlateral setae; elytral mirrors present on interval 3, in some specimens on intervals 4 and 5, but not on intervals 6 through 8; aedeagus slender, with narrow basal orifice (Fig. 117).

Comparisons with related species.– From the externally similar *B. lapponicum* and *B. velox*, males can be best separated by characters of the aedeagus, and females by the elongate second stylomeres (longer than 400 µm in *B. carinula*, around 200 µm in *B. velox* and *B. lapponicum*). Aedeagus of *B. carinula* slenderer, with narrower basal orifice; right lobe of CSC unridged; ostial microtrichial patch smaller; with no dorsal field; dorsal plate with small sclerotized patch with dark, irregular borders; other *Chrysobracteon* have dark dorsal plates (most notably *B. hesperium*), but in these the sclerotized region is more extensive. *B. carinula* members can be externally distinguished from *B. lapponicum* by the long basilateral pronotal carina, more convex pronota with more-rounded sides and less-divergent hind angles, and relatively narrower elytral interval 3. From *B. velox*, by the pronotal carina.

Some specimens of *B. carinula* have been confused with *B. balli*, especially old, worn, *B. carinula* in which the mirrors are invisible or unclear; the basilateral pronotal carina and genitalia are the best distinguishing features.

Description.– As in Table 2, plus: *Size*. SBL = 4.4-6.4mm. *Color*. Dorsal surface bronze, grey-bronze, coppery-red, dark bluish, or aeneous; mirrors in many specimens purplish or reddish; silver spots aeneous, blue, or bronze. Appendages in most specimens pale, with first four antennomeres rufotestaceous ventrally and basally, palpi partly pale, and legs rufotestaceous, femora and tibiae infuscated apically, tarsi dark. Other specimens, especially from Alberta and Saskatchewan, have the femur and tibia more extensively infuscated; in some only the bases of the femora are pale. *Microsculpture*. In general shinier than both *B. velox* and *B. lapponicum*. Pronotum frequently shinier than elytra. Mirrors on interval 5, when present, not more evident than on 4. *Thorax*. Pronotum convex, sides sinuate, more definitely rounded than most specimens of *B. velox* or *B. lapponicum*; hind angle right or obtuse in many specimens. *Elytron*. Humeral margin long, extended to interneur 5 or nearly so; interneurs slightly to moderately impressed; interval 3 relatively narrow, not much wider than 2. *Female genitalia*. Spermatheca as in Fig. 170, with relatively short and straight cornu, and long, flat basal portion. Spermathecal duct with posterior lobe at base. Stylomeres as in Fig. 154. Sternum X dark, asetose, clothed with small pegs (Fig. 185).

First instar larva (Figs. 197, 198, 213, 228, 234, 243, 246, 250, 253, 256)

Diagnostic combination.– Head centrally darker, frontale without spots (Fig. 213); large, stout, closely set parietal egg bursters (Figs. 228, 234), PR_{13}, ME_{14}, and TE_{11} very short (Fig. 250); FR_1, FR_3, and segment VIII EP_1 as wide as nearby setae (Figs. 197).

Comparisons with related species.– From the species with most similar larvae, *B. alaskense*, distinguished by the exceptionally large egg bursters and sensillar characters mentioned in the diagnosis.

Description.– As in Table 2, plus: *Size.* LHw = 450-460 µm, LHl = 340-360 µm, LCl/LHl = .094-.104. Four specimens measured. *Color.* Head pale with center diffusely darker, and with dark spot on center of frontale, or more generally pale brown. *Microsculpture.* Frontale lacking pointed microsculpture (although two of the eight specimens studied had a few small denticles posteriorly). Mandibles lacking microsculpture (compare Fig. 198 with Figs. 199 and 239). *Sensilla.* Unlike most *Chrysobracteon*, FR_5 is anterior to FR_4 in most specimens.

Second instar larva (Fig. 260)

Description.– LHw = 630-665 µm (n=2). Frontale with extra setae near FR_3, and lacking microsculpture posteriorly. Head and pronotum with accessory microsetae short, less than two times longer than wide. Microsculpture absent centrally on pronotum. Urogomphus with ten long setae

(Fig. 260).

Specimens examined.– I have seen 2248 adults, 57 first instars, and 4 second instars from the following collections: AMNH, AMor, BJCa, BMNH, CAS, CNC, CUIC, DHKa, DRMa, FMNH, GDND, HNHM, ICCM, JKLi, KUSM, MCZ, OSUO, ROM, SAEl, SMNH, UASM, UBC, UCB, UMHF, UMSP, UMMZ, USNM, ZIL.

Geographic distribution.– A common species, distributed from Newfoundland and New Jersey in the east, south to Kentucky, west to Iowa, British Columbia, and north to southeastern Yukon and western N.W.T. (Fig. 265). I have seen three specimens, probably mislabeled, with the following labels: "Or." (USNM), "Tex" (MCZ), and "ARIZONA Pena Blanca 20.VIII.1966" (AMNH). Lindroth's (1963:237) record from Washington is based on a misidentified *B. lapponicum* (OSUO!).

Geographic variation.– Populations from west of Manitoba have a higher frequency of dark appendages; those from northern British Columbia and southern Yukon in general are more heavily microsculptured, with less regular basilateral carinae of pronota, and less convex pronota.

Habitat.– This species often occurs on upper, dry sand banks of rivers and lakes. In Manitoba and eastward, it seems restricted to lake banks, but occurs frequently along large rivers in Saskatchewan and westward.

Phylogenetic relationships.– There is conflicting evidence as to the relationships of *B. carinula*; some characters ally it with the *B. argenteolum*-subgroup, others with *B. lapponicum*. I consider it tentatively to be the sister group of *B. lapponicum* plus *B. velox*.

4.4.8 *Bembidion velox* (Linné)

Carabus velox Linné, 1761:222. TYPE material lost (see Lindroth 1957:335,339). Type locality Fårö Island near Gotland, Sweden.

Elaphrus impressus Panzer, 1797, number 8. Location of type unknown. Type locality Germany.

Elaphrus striatus Paykull, 1798:175 (not Fabricius 1792:179). Type presumably in Paykull collection, Naturhist. Riksmus., Stockholm (Horn and Kahle 1937). Type locality Sweden.

Bembidium Güntheri Seidlitz, 1887:64. Location of TYPE unknown, according to Lindroth (1962:13). Type locality Petrosavodsk, U.S.S.R..

(*Bembidion velox* v. *semicyaneum* Meier, 1899:97. [Name unavailable as clearly intended to be infrasubspecific.])

(*Bembidium velox* L. ab. s. *bimaculatum* Uyttenboogaart 1904:172 (*nec* Kirby 1837:52). [Name unavailable as clearly intended to be infrasubspecific.])

(*Bembidium velox* ab. *nigrescens* Kuhnt, 1913:57. [Name unavailable as clearly intended to be infrasubspecific.])

(*Bembidion velox* ab. *moestum* Csiki, 1928:37; new name for *Bembidium velox* ab. *nigrescens* Kuhnt 1913. [Name unavailable as clearly intended to be infrasubspecific.])

(*Bembidion velox* ab. *Evertsi* Csiki, 1928:37; new name for *Bembidium velox* ab. s. *bimaculatum* Uyttenboogaart 1904. [Name unavailable as clearly infrasubspecific.])

Derivation of specific epithet.– From the Latin "*velox*", meaning "swift", referring no doubt to the rapid running of members of this typical *Chrysobracteon* species, and the speed with which they take flight.

Adult (Figs. 13, 118, 135, 155, 171)

Diagnostic combination.– Elytral interval 3 with distinct mirrors, in some specimens on 2 through 5 as well; pronotum without long basilateral carina; if basilateral carina present, then short, not extended to pronotal base, midlateral seta present. Aedeagus with right lobe of CSC ridged and far removed from basal orifice (Fig. 118); ostial microtrichial patch extended dorsally as a prominent dorsal field of long microtrichia; left-most central membranes with small, sparse, heavily sclerotized scales, sac thus with a peppered appearance; "pillow" with large scales lacking.

Comparisons with related species.– The short basilateral carina of pronotum, isolated from the base, distinguishes adults of this species from those of *B. carinula*. As well, the elytra of *B. velox* are generally narrower and more nearly parallel-sided. Aedeagal characters of *B. velox*, as noted in the diagnoses, are also distinctive. Differences from *B. lapponicum* are given under that species.

Description.– As in Table 2, plus: *Size*. SBL = 4.6-6.0mm. *Color*. Dorsal surface dull bronze, coppery, aeneous, or bluish; mirrors coppery red or purplish, silver spots aeneous, bluish, or bronze. Appendages in most specimens pale; antennomere 1 entirely pale, or infuscated dorsally, antennomeres 2 through 4 pale basally; palpi dark apically, maxillary palpomere 2 pale; legs rufous, slightly infuscated at joints and on tarsi. *Thorax*. Pronotum similar to that of *B. carinula*, with sides less rounded in most specimens. *Elytron*. Humeral margin long, to interval 5 or beyond; interneurs slightly to moderately impressed; interval 3 relatively narrow. *Female genitalia*. Spermatheca with short, apically hooked cornu, more tapered than in *B. lapponicum*; basal portion long, flat (Fig. 171). Spermathecal duct with no posterior lobe. Stylomeres as in Fig. 155.

First instar larva

Unknown.

Specimens examined.– I have seen 195 adults from the following collections: AMNH, BMNH, CAS, CNC, HNHM, ICCM, MCZ, UMHF, USNM, ZMLS.

Geographic distribution.– In the Palearctic from western France to Scandinavia, north of the Alps, east to the Irtysh and Jenesei Rivers of the U.S.S.R. (Netolitzky and Meyer 1939, Lindroth 1962, Fig. 266).

Geographic variation.– None observed.

Habitat.– On pure, completely barren sand (Lindroth 1945). On larger lakes and river banks; also on banks of bodies of salt water (for example, the Baltic Sea (Lindroth 1945)).

Phylogenetic relationships.– The inconclusive evidence available suggests a relationship with *B. lapponicum* (Fig. 278).

4.4.9 *Bembidion lapponicum* Zetterstedt

Bembidium impressum Var. b. *lapponicum* Zetterstedt, 1828:6. LECTOTYPE male selected by Lindroth 1963:239, in UML. Type locality Vittangi on Torne-älve, Sweden.

Bembidium latiusculum Motschulsky, 1845:272. TYPE material apparently lost, according to Lindroth (1962:13); Keleinikova (1976) does not include this name in her catalogue of the Motschulsky collection in Moscow. Type locality "en Dauria et au Kamtchatka", restricted to

"'Dauria', that is Transbaicalia, Siberia" by Lindroth (1962:13).

Bembidium Jenisseense J. Sahlberg, 1880:14. LECTOTYPE female selected by Lindroth 1963:239, in UMT. Type locality Imbatsk, Lower Jenissei, U.S.S.R..

Bembidium pugetanum Fall, 1916:13. HOLOTYPE male, examined, in MCZ. Labeled: "Seattle Wash O.B.J. [hand written] / TYPE pugetanum / M.C.Z. Type 23865 [red label] / H.C. FALL COLLECTION". Type locality Seattle, Washington.

Derivation of specific epithet.– From "Lapponia", or Lapland.

Adult (**Figs. 14, 44, 46, 51, 59, 61, 71, 119, 136, 156, 172**)

Diagnostic combination.– Elytra with mirrors on interval 3, in most specimens with fainter mirrors on 2 through 5, rarely with very faint mirrors on 6 and 7; pronotum without long basilateral carina, with midlateral seta, and with hind angles prominent, flared outward (Fig. 14); aedeagus wide and short, with one prominent apical lobe (the "pillow") with large triangular scales (Fig. 119).

Comparisons with related species.– Difficult to distinguish using external characters from *B. velox*, and to a lesser extent, *B. carinula*. The prothorax of *B. lapponicum* is flatter, with less rounded sides, and broader base with more protruded hind angles. Generally silver spots are wider and longer, with the interval 3 wider as well. Legs are darker in most specimens. Aedeagus wider and much shorter than in *B. velox* and *B. carinula*; right lobe of CSC ridged as in *B. velox*, but the lobe is more basal, nearly touching the basal orifice; ostial microtrichial patch large, posteriorly with many comb-like scales extended upward as the dorsal field; central membranes not peppered, as scales are larger and less sclerotized; apically, the "pillow" is covered with large triangular scales; other *Chrysobracteon* have similarly positioned lobes, but no other has such distinctive scales.

Description.– As in Table 2, plus: *Size*. SBL = 4.5-6.1mm. *Color*. Dorsal surface bronze, grey-bronze, bluish, or aeneous; mirrors purplish or coppery; silver spots aeneous, bluish, or bronze. Appendages dark, piceous, except for venter of antennomere 1, and femur at base, which are rufous or rufopiceous; some specimens have as well paler tibiae. *Sensilla*. Midlateral setae of pronotum present, rarely absent; only one specimen seen (from "Maalselven, Framnes", ZMLS!) without setae. *Thorax*. Side margins of pronotum sinuate, little rounded, hind angles prominent, flared outward, acute in most specimens; basilateral carina thin, generally short, never extended to basal edge of pronotum. *Elytron*. Humeral margin long, extended to inward of interneur 5, longer than in *B. carinula*; interneurs slightly to moderately impressed; interval 3 wide, especially around silver spot. *Female genitalia*. Spermatheca with long, distinctly curved cornu; basal portion long, flat (Fig. 172). Spermathecal duct with or without small posterior lobe. Stylomeres as in Fig. 156.

First instar larva (Figs. 206-209, 214, 229, 235)

Diagnostic combination.– Head capsule dark, without traces of spots on frontale (Fig. 214); prominent parietal denticles (Fig. 229, 235); setae ME_2 and TE_6 short, scale-like; seta ST_2 on segment IX present.

Comparisons with related species.– From the similarly dark *B. balli* and *B. foveum*, distinguished by the shorter coronal suture and more prominent parietal denticles, as well as the short ME_2 and TE_6.

Description.– *Size*. LHw = 400-425 µm, LHl = 330-350 µm, LCl/LHl = .114-.129. Three specimens measured. *Color*. Head capsule dark, piceous, more or less uniform, or frontale darker centrally, paler laterally; parietale darker in front of PA_6 and PA_7.

Second instar larva (Fig. 259)

Description.– LHw = 540 µm (n=1). Frontale without extra setae near FR_3, and lacking microsculpture posteriorly. Head and pronotum with accessory microsetae short, less than two times longer than wide. Microsculpture absent centrally on pronotum. Urogomphus with nine long setae (Fig. 259).

Specimens examined.– I have seen 366 adults, 33 first instars, and 2 second instars from the following collections: AMNH, AMor, BMNH, CAS, CNC, DRMa, HNHM, ICCM, MCZ, OSUC, OSUO, UASM, UMHF, USNM, ZMLS.

Geographic distribution.– A widespread Holarctic species (Fig. 267, Lindroth 1962), in the Old World from northernmost Scandinavia throughout much of the U.S.S.R., south to Mongolian Peoples' Republic, east to Kamtchatka. In North America (Fig. 267b) common in the northwest, from Alaska east to the Anderson River; uncommon at in scattered localities in the south from Washington, Oregon, Idaho, and Wyoming, east to central Saskatchewan.

Geographic variation.– Populations from the southern portion of the range in North America (central B.C., Alberta, and Saskatchewan southward) are more uniform than northern populations. Southern specimens are larger, with straighter, less-impressed interneurs, a generally smoother and shinier surface, with mirrors on interneurs 2, 4, and 5 generally absent or very faint, and with a relatively narrow interval 3; some northern specimens are like this as well. The male genitalia appear identical to those of northern specimens. Unfortunately, the relative lack of collecting throughout much of the northern portions of British Columbia, Alberta, and Saskatchewan makes interpretation of this form difficult: it is unknown if the southern form is allopatric or sympatric with the northern form, or if a cline connects them. Further work may reveal the distinctiveness of the southern form, if so, it would take on the epithet "*pugetanum* Fall", most likely as a subspecies of *B. lapponicum*.

The material I have at hand is too limited to identify clear patterns of variation in the Old World. Lindroth (1962) gives a brief discussion of Palearctic variation.

Habitat.– Generally on barren sand banks of large rivers, less frequently around small rivers, and rarely around lakes (Lake Brooks, Alaska).

Phylogenetic relationships.– Apparently the sister species of *B. velox* (Fig. 278).

4.4.10 *Bembidion punctatostriatum* Say

Bembidium punctato-striatum Say, 1823b:83. NEOTYPE male designated by Lindroth and Freitag (1969:335), examined, in MCZ, labeled: "Rumney, N.H. V.51 Lindroth / Neotypus Bembidium punctatostriatum Say design Lth [red label, in Lindroth's handwriting] / Bembidion punctatostriatum Say det. Lindroth 68". Type locality Rumney, New Hampshire, designated by Lindroth 1962:12.

Bembidium sigillare Say, 1834:437. TYPE material lost, see Lindroth and Freitag (1969:335). Type locality "Missouri" (probably present-day Nebraska, according to Lindroth 1969:1113).

Bembidium stigmaticum Dejean, 1831:83. TYPE, examined by Lindroth (1962:12), in MNP. Type locality: "Amérique septentrionale".

Derivation of specific epithet.– From the Latin "*punctum*", meaning puncture, and "*stria*", meaning furrow or line, referring to the punctate interneurs of this species.

Adult (Figs. 11, 33, 34, 45, 48, 52, 60, 67, 72, 94, 120, 137, 153, 173)

Diagnostic combination.– Long and wide (Fig. 11); surface shiny, mirrors present on interval 3, but not on 6 and 7; mentum tooth parallel-sided, truncate, bulbous; prothorax with wide base and little-rounded sides (Fig. 11), with midlateral seta; humeral margin of elytra prominent, long, extended to interneur 5 (Fig. 72); ostial patch of simple microtrichia large (Fig. 120).

Comparisons with related species.– A distinctive species, not liable to be confused with other species. From the somewhat similar *B. lorquinii* distinguished externally by the wider body and presence of midlateral pronotal seta, and aedeagally by the usually unridged right CSC lobe and the prominent dorsal VSP ridge.

Description.– As in Table 2, plus: *Size*. SBL = 4.9-7.1mm, rarely below 5.5mm. *Color*. Dorsal surface bronze or silver grey, mirrors coppery red or purplish, silver spots aeneous. Antennomere 1 ventrally pale; legs dark, piceous or black, with base of femora, pro- and mesotrochanters, as well as tibiae in most specimens, rufous or rufopiceous. *Thorax.* Pronotum with slightly sinuate sides and wide base (about as wide as maximum width anterior to hind angles). *Elytron.* Humerus prominent, with margin long, extended to interneur 5; interneurs shallow to moderately impressed. *Female genitalia.* Spermatheca quite varied, in many specimens as in Fig. 173; cornu curved or not, generally fairly long. Spermathecal duct with distinct bulb at base, but no posterior lobe. Stylomeres as in Fig. 153.

First instar larva (Figs. 194, 204, 215, 230, 237, 239, 241, 251, 254)

Diagnostic combination.– Head broad, pale, with 3-spotted frontale and 2-spotted parietale (Fig. 215); parietal denticles small; seta FR_3 thick but FR_1 thin; pronotum with extensive tubercles set in rows; basilateral corners of thoracic tergites with several extra small setae (setal groups gPR and gME, Figs. 237, 241), and posterolateral corner of abdomen with extra seta (TEα, Fig. 251).

Comparisons with related species.– The distinctly spotted head, microtuberculate pronotum, and setal groups gPR and gME combine to make *B. punctatostriatum* first instar larvae distinctive and unlikely to be misidentified.

Description.– As in Table 2, plus: *Size.* LHw = 440-505 μm, LHl = 370-390 μm, LCl/LHl = .128-.130. Three to five specimens measured.

Second instar larva

Description.– LHw = 730 µm (n=1). Frontale without extra setae near FR_3, and with microsculpture posteriorly. Head and pronotum with accessory microsetae less than two times longer than wide. Microsculpture present centrally on pronotum. Urogomphus with seven long setae.

Specimens examined.– I have seen 425 adults, 70 first instars, 1 second instar, and 1 third instar from the following collections: AMNH, BJCa, BMNH, CAS, CNC, CUIC, DHKa, DRMa, ICCM, JKLi, KUSM, MCZ, OSUC, OSUO, ROM, SMNH, UASM, UBC, UMMZ, USNM, ZIL.

Geographic distribution.– In the New World from New Brunswick and Maine south to Kentucky and Arkansas (Lindroth 1962); in the west from Saskatchewan and Montana, to the Yukon, and Fort MacPherson, N.W.T.; apparently absent from the center of the continent (Fig. 268). I have seen three specimens labelled "TEX" (OSUC, USNM), and two labelled "Cal." (MCZ); both are doubtful records.

Geographic variation.– None noted.

Habitat.– On the barren sand banks of large and small rivers, as well as lakes. Specimens frequent drier areas of the sand banks; on the North Saskatchewan River near Paynton, Saskatchewan, found at a considerable distance from the water.

Phylogenetic relationships.– *B. punctatostriatum* has proven to be the most difficult *Chrysobracteon* to place phylogenetically. It shows ties with the *B. argenteolum*-subgroup, *B. lapponicum*, and the *B. inaequale*-subgroup; I have left it unplaced within the mirrored *Chrysobracteon* (Fig. 278).

4.4.11 *Bembidion hesperium* Casey

Bembidium hesperum Fall, 1910:95 (not Crotch 1867:385).
HOLOTYPE male, examined, in MCZ. Labeled: "Vanc. Id. 8/24/96 / hesperum TYPE [hand-written] / M.C.Z. Type 23862 [red label] / H.C. Fall Collection". Type locality Vancouver Island, British Columbia.

Bembidion hesperium Casey, 1918:9. New name for *B. hesperum* Fall.

Bembidion binarium Casey, 1918:9. LECTOTYPE male designated by Lindroth 1975:115, in USNM. Type locality: California.

Derivation of specific epithet.– From the Latin "*hesperius*", meaning "western" or "of the evening". This lovely name might refer to either the place of residence of these animals, the western edge of North America, or to their dark tone.

Adult (Figs. 15, 53, 64, 95, 121, 138, 157, 174)

Diagnostic combination.– Dark, shiny, mirrors thus somewhat obscured (Fig. 15), present on intervals 3 through 5; dorsal surface of elytra with sculpticells generally transverse (isodiametric only in deeply microsculptured females) (Fig. 64); pronotum with carina short or absent, lacking midlateral seta; interneur 3 abruptly deeper around silver spots; basal portions of femora rufous; aedeagus with wide apex, right CSC lobe at most slightly ridged (Fig. 121).

Comparisons with related species.– Adults of this species are the darkest *Chrysobracteon*, and, along with *B. semenovi*, the shiniest. Most similar to *B. lorquinii*, with which it shares the lack of the midlateral seta of the pronotum. Besides luster, color, and genitalia, specimens can be distinguished by the more deeply engraved and punctate interneurs, smaller size, and proportionally wider body. Genitalic differences are described under *B. lorquinii*.

Description.– As in Table 2, plus: *Size*. SBL = 4.7-5.8mm. *Color*. Dorsal surface dark, with aeneous, bluish green, or bronze tint; mirrors coppery or purplish red; silver spots aeneous or bluish green. Appendages dark, for the most part piceous; antennomere 1 rufous ventrally; in most specimens basal portions of femora are rufous as well. *Thorax*. Pronotum with sides slightly sinuate. *Elytron*. Humerus somewhat rounded, margin short, extended to interneur 6 but not 5; interneurs slightly to moderately impressed; third deepened abruptly around silver spots. *Female genitalia*. Spermatheca as in Fig. 174; cornu fairly short, only slightly curved. Spermathecal duct without posterior lobe. Stylomeres as in Fig. 157.

First instar larva

Diagnostic combination.– As for *B. lorquinii*, except that there is virtually no microsculpture near coronal suture. No other differences noted. *Size*.– LHw = 350-360 µm, LHl = 255-270 µm, LCl/LHl = .109-.111. Two specimens measured. See Table 2 for full description.

Second instar larva

Description.– As for *B. lorquinii*; LHw = 540 µm (n=2).

Specimens examined.– I have seen 417 adults, 52 first instars, 7 second instars, and 1 third instar from the following collections: AMNH, BJCa, BMNH, CAS, CNC, DHKa, DRMa, FMNH, GDND, HNHM, ICCM, MCZ, OSUO, UASM, UBC, USNM, ZIL.

Geographic distribution.– Restricted to the westernmost states, from around San Francisco, California, north to Washington, and in southernmost British Columbia (Fig. 269).

Geographic variation.– Specimens from the south (*e.g.* Klamath River, northern California, DRMa!) tend to be shinier, with more-transverse elytral sculpticells, and with flatter pronota with less rounded sides than specimens from the north (*e.g.* Nooksack River, northern Washington, DRMa!).

Habitat.– Known only from the sandy banks of rivers; occasionally among vegetation.

Phylogenetic relationships.– A primitive member of the 2n=20+XY clade; its sister group is not known (Fig. 278).

4.4.12 *Bembidion lorquinii* Chaudoir

Bembidium lorquinii Chaudoir, 1868:239. LECTOTYPE male designated by Lindroth 1963:235, in MNP. Type locality California.

B. lorquini auctorum.

Bembidion tacomae Casey, 1924:22. LECTOTYPE male designated by Lindroth 1975:115, examined, in USNM. Labeled: "Wawawai Wn [hand written] / CASEY bequest 1925 / TYPE USNM 36797 [red label] / tacomae Csy [hand written] / LECTOTYPE tacomae Csy By C.H. Lindroth". Type locality Wawawai, Washington.

Notes about synonymy.– "*Bembidion lorquini*" is an incorrect subsequent spelling (ICZN, Third Edition, Art. 33(d)).

Derivation of specific epithet.– Patronym honoring M. Lorquin, who sent the type series to M. H. Deyrolle, from whom the Baron Chaudoir received them.

Adult (Figs. 16, 122, 139, 158, 175)

Diagnostic combination.– Duller than *B. hesperium* (Fig. 16), with mirrors on intervals 3 through 5; elytral sculpticells isodiametric; pronotum with carina short or lacking, and without midlateral seta; interneur 3 not as abruptly deepened around silver spots; femora black or piceous; aedeagus with ridged right CSC lobe, otherwise as in Fig. 122.

Comparisons with related species.– A large species, similar to *B. hesperium*. It is larger, more slender, and with a duller luster than specimens of that species. In addition, the interneurs of *B. lorquinii* are shallower, especially around the silver spots, and the punctures are smaller; ed3 and ed5 in smaller pit than in *B. hesperium*; apex of aedeagus narrower than in *B. hesperium*; right lobe elongate, consistently markedly ridged (at most only slightly so in *B. hesperium*); ostial microtrichial patch larger than in *B. hesperium*, with more extensive dorsal field; VSP with slightly more prominent, angulate dorsal ridge.

Description.– As in Table 2, plus: *Size.* SBL = 5.3-6.8mm. *Color.* Dorsal surface greenish-grey, grey-bronze, or bronze; mirrors purplish, coppery, or bronze; silver spots greyish, bronze, or aeneous. Appendages very dark, black or piceous, with only the pro- and mesotrochanters paler, rufopiceous. *Thorax.* Pronotal side margins little sinuate; basilateral tubercle prominent. *Elytron.* Humeral margin short, extended to interneur 6 but not 5; interneurs slightly to moderately impressed, not abruptly deepened around silver spots. *Female genitalia.* Spermatheca varied, in many specimens as in Fig. 175. Spermathecal duct without posterior lobe. Stylomeres as in Fig. 158.

First instar larva (Fig. 216)

I have not been able to distinguish larvae of *B. lorquinii* from most members of the *B. inaequale*-subgroup. The description below thus applies, with a few exceptions, to *B. lorquinii*, *B. zephyrum*, *B. levettei*, and *B. inaequale*.

Diagnostic combination.– Head pale, with 3-spotted frontale, spots indistinct in some specimens (Fig. 216); parietale with small denticles, with denticulate microsculpture near coronal suture; pronotum lacking microsculpture; ME_2 and TE_6 large.

Comparisons with related species.– *B. lorquinii* and *B. inaequale*-subgroup larvae are most similar to those of *B. balli* and *B. foveum*. However, the former have paler head capsules, with more prominently denticulate frontales, and lack lateral pronotal microtubercles.

Description.– As in Table 2, plus: *Size.* LHw = 380-390 µm, LHl = 295-300 µm, LCl/LHl = .119-.133. Two specimens measured.

Second instar larva

Description.– LHw = 550 µm (n=1). Frontale without extra setae near FR_3, and lacking microsculpture posteriorly. Head and pronotum with accessory microsetae clearly over three times longer than wide. Microsculpture absent centrally on pronotum. Urogomphus with seven long setae.

Specimens examined.– I have seen 389 adults, 16 first instars, and 2 second instars from the following collections: AMNH, BHar, BMNH, CAS, CNC, CUIC, DHKa, DRMa, FMNH, HNHM, ICCM, JKLi, MCZ, OSUO, UASM, UBC, UCB, UMMZ, USNM, ZIL.

Geographic distribution.– Similar to that of *B. hesperium*, but with an extension farther eastward. From near Los Angeles, California, east to western Nevada, north to Idaho and southwesternmost British Columbia (Fig. 270). I view the record from Colorado (Lindroth 1963, USNM!) with suspicion.

Geographic variation.– None noted.

Habitat.– Generally found on barren sandy banks of rivers. One population has been found near seepage on sandy Wreck Beach, on the Pacific Ocean banks of Vancouver, B.C. (BHar!). The water here is at least brackish, if not saline (B. Harrison, pers. comm.), making this population the only known *Chrysobracteon* found next to salty water other than *B. zephyrum* and *B. velox*.

Phylogenetic relationships.– *B. lorquinii* belongs to the 2n=20+XY clade, but its exact relationships with *B. hesperium* and the *B. inaequale*-subgroup are unresolved (Fig. 278).

B. inaequale-subgroup

Contained herein are the remaining five species of *Chrysobracteon*. All have extensive elytral mirrors, straight CSC flagella, 10 autosomal pairs, and similar larvae.

4.4.13 *Bembidion zephyrum* **Fall**

Bembidium zephyrum Fall, 1910:96. HOLOTYPE male, examined, in MCZ. Labeled: "Humboldt Co. CAL. / [male symbol] / zephyrum TYPE [hand-written] / M.C.Z. Type 23870 [red label] / H.C. Fall Collection / Bembidium zephyrum Fall". Type locality Humboldt County, California.

Bembidion zephyrum tristiculum Casey, 1924:22. LECTOTYPE male designated by Lindroth 1975:115, examined, in

USNM. Labeled: "S. Oregon Kunf [spelling?] [hand written] / CASEY bequest 1925 / TYPE USNM 36795 [red label] / tristiculum Csy [hand written] / LECTOTYPE sbsp. tristiculum Csy By C.H. Lindroth". Type locality southern Oregon.

Bembidion marginosum Casey, 1924:23. LECTOTYPE male designated by Lindroth 1975:115, examined, in USNM. Labeled: "Del Norte Co. CAL VI.2.10 / CASEY bequest 1925 / marginosum Csy [hand written] / TYPE USNM 36793 [red label] / LECTOTYPE marginosum Csy By C.H. Lindroth". Type locality Del Norte County, California.

Derivation of specific epithet.– From the Latin "*zephyrus*", meaning "west wind". The beaches these beetles inhabit are swept over by winds blowing from the west across the Pacific Ocean.

Adult (Figs. 19, 54, 79, 82, 84, 123, 140, 159, 176)

Diagnostic combination.– Wide, relatively flat; with prominent raised mirrors on intervals 2 through 7, in pattern of Fig. 19; connection between anterior elytral mirrors and central mirrors absent or consisting of only a very thin mirror on interval 3; pronotum with carina small or absent, with wide lateral expansion and flared front angles; midlateral pronotal seta present; aedeagus with very broad ostial microtrichial patch; VSP with rounded, unscaled dorsal ridge (Fig. 123).

Comparisons with related species.– Rather similar to *B. levettei*, with which it has been confused in the past. Specimens of *B. zephyrum* are generally brighter than those of *B. levettei*, with the copper or purple mirrors contrasted against the generally green or blue-green elytra. The mirror of the anterior portion of intervals 3 through 5 is connected to the more posterior mirrors only by a faint band on the interval 3 (Fig. 19) in related species (for example, *B. levettei*, Fig. 20) this band is a much more definite mirror. Mentum tooth not bulbous, against *B. levettei* and *B. inaequale*; mental incisions not as deep or outwardly directed as in *B. levettei* and *B. inaequale*; submentum with 4 setae, as medial setae absent, in contrast to 6 setae in *B. levettei*. The side margin of the pronotum is more explanate than in most specimens of related species; it flares out into a protruded front angle. Protarsomere 1 of males is noticeably wider and thicker than in *B. levettei* (compare Figs. 79 and 82 with 80 and 83), as are the associated adhesive setae (compare Fig. 84 with 85). Ostial microtrichial patch extensive, with apical comb-like scales, and a prominent dorsal field of microtrichia. VSP usually without the distinctly angulate and sclerotized dorsal ridge of *B. levettei* and other members of the group, dorsal ridge not angulate.

Description.– As in Table 2, plus: *Size*. SBL = 5.0-6.3mm. *Color*. Dorsal surface generally bluish green, although some specimens aeneous, with purplish, coppery red, or purplish black mirrors; this same contrast in color between shiny and dull areas of the elytra is also true of the pronotum. Appendages dark, piceous except for rufous pro- and mesotrochanters and base of femora. *Microsculpture.* Pronotum with distinct shiny band on disc on each side close to midline; in some females outer mirrors rather faint, or, rarely, virtually absent (one female from Siltcoos Outlet, Oregon, OSUC!); interval 7 mirror connected to inner mirrors, although the connecting interval 6 mirror is occasionally faint or small. *Thorax.* Pronotum wide, relatively flat, lateral margins expanded as protruded front angles. *Elytron.* Humerus somewhat rounded, short, not extended to interneur 5; interneurs slightly to moderately impressed. *Female genitalia.* Spermatheca as in Fig. 176; cornu distinctly curved. Spermathecal duct without posterior lobe. Stylomeres as in Fig. 159, of varied lengths (Fig. 3).

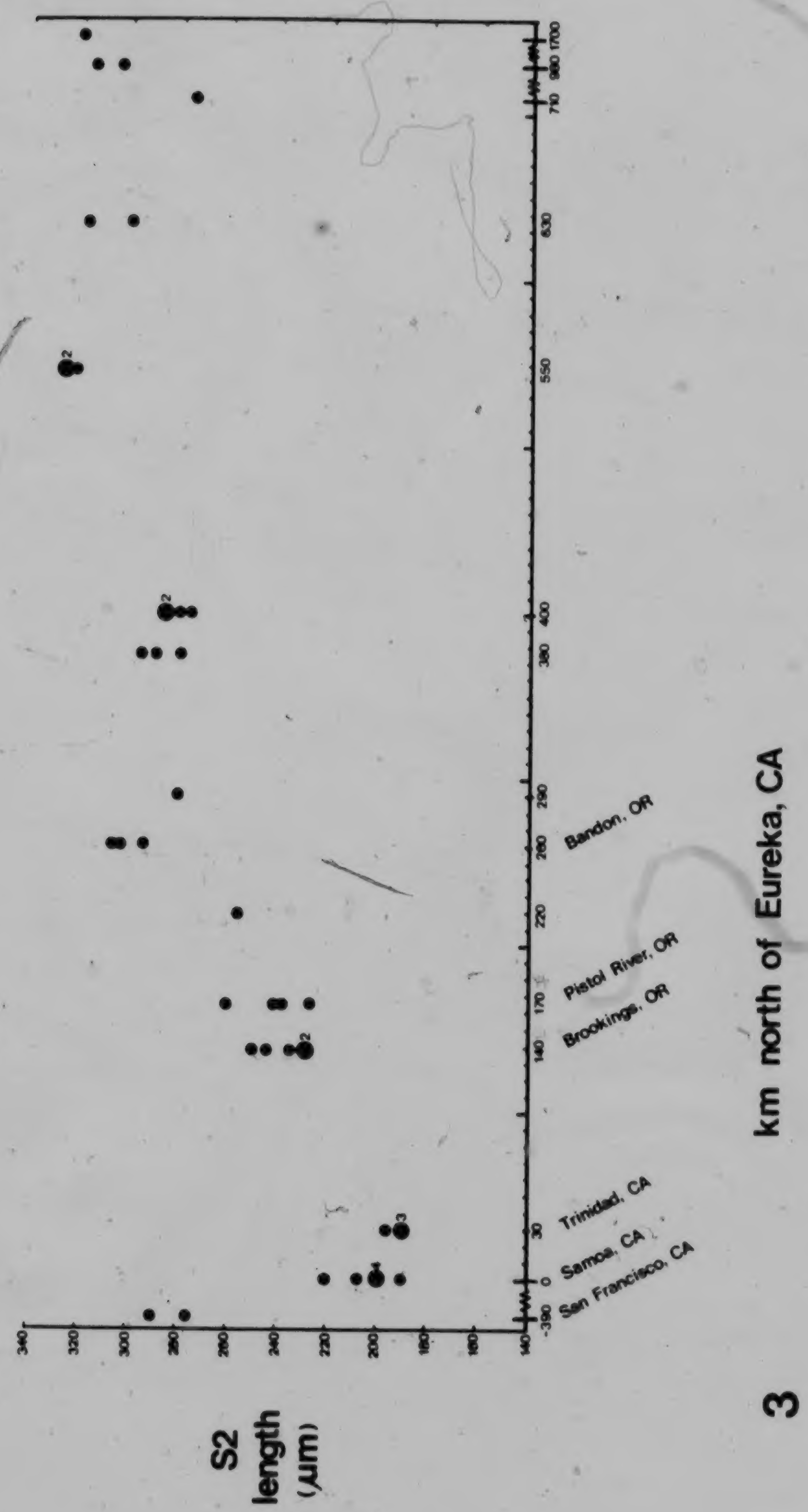
First instar larva (Fig. 217)

Diagnostic combination.– As for *B. lorquinii*, except color paler, flavous; head generally, but not always, with distinct spotted pattern. *Size.*– LHw = 380-410 µm, LHl = 315-320 µm, LCl/LHl = .117-.119. Two specimens measured. See Table 2 for full description.

Second instar larva

Description.– As for *B. lorquinii*.

Figure 3. Geographic variation of *B. zephyrum* female second stylomere length.


S2 length (μm)
340
320
300
280
260
240
220
200
180
160
140
km north of Eureka, CA
-390
0
30
140
170
220
260
290
380
400
550
630
710
980
1700
San Francisco, CA
Samoa, CA
Trinidad, CA
Brookings, OR
Pistol River, OR
Bandon, OR
2
3
2
2
2

3

Specimens examined.– I have seen 1162 adults, 22 first instars, and 1 second instar from the following collections: AMNH, BJCa, BMNH, CAS, CNC, CUIC, DHKa, DRMa, FMNH, HNHM, MCZ, OSUO, UASM, UBC, UCB, UMSP, UMMZ, USNM, ZIL.

Geographic distribution.– Found mainly on the Pacific coast of North America, from San Francisco to the Queen Charlotte Islands (Fig. 271); only a few specimens have been found at inland localities. Inland specimens from Creston, B.C., reported by Lindroth (1962,1963) as *B. zephyrum*, are actually members of *B. levettei levettei* (CNC, UBC!).

Geographic variation.– None noted in external features. However, the length of S2 in females varies considerably (from 190 µm to 325 µm); this variation is correlated with geography (Fig. 3), but not with body length. Except for the only two known *B. zephyrum* females from central California (San Francisco) (CAS!), Californian specimens have shorter S2's than do specimens from Bandon, Oregon, and northward; southernmost Oregon is a zone of intermediates. I do not feel that this diversity warrants use of subspecific names.

Habitat.– For the most part restricted to sandy beaches of the Pacific Ocean, where it is sometimes abundant under driftwood.

Phylogenetic relationships.– Apparently the sister group of the rest of the *B. inaequale*-subgroup (Fig. 278).

4.4.14 *Bembidion levettei* Casey

Bembidion levettei Casey, 1918:9. LECTOTYPE male designated by Lindroth 1975:114, examined, in USNM. Labeled: "Col / CASEY bequest 1925 / TYPE USNM 36793 [red label] / levettei Csy [hand-written] / LECTOTYPE levettei Csy By C.H. Lindroth". Type locality Colorado.

Bembidion carrianum Casey, 1924:23. LECTOTYPE female designated by Lindroth 1975:115, examined, in USNM. Labeled: "Edmonton Alta 1.VII.1920 F.S. Carr / CASEY bequest 1925 / carrianum Csy [hand-written] / TYPE USNM 36800 [red label] / LECTOTYPE carrianum Csy By C.H. Lindroth". Type locality Edmonton, Alberta.

Derivation of specific epithet.– Patronym honoring "Levette", from whose collection the types originated.

Adult (Figs. 20, 21, 55, 80, 83, 85, 103-106, 111, 124, 125, 141, 160, 161, 177, 180-182)

Diagnostic combination.– Mirrors on intervals 2 through 7, in pattern of Figs. 20-21; anterior elytral mirrors generally connected to middle mirrors by a broad mirror on interval 3; mirrors on intervals 6 and 7 located nearer anterior silver spot, broadly connected to inner mirrors; pronotum with carina short or absent, front angle not flared outward, midlateral seta present; VSP with both basins and dorsal ridge scaled (a few specimens lack or have only very small scales) (Figs. 124-125).

Comparisons with related species.– Many specimens confused with the other two North American species with mirrors on elytral intervals 6 and 7, *B. zephyrum* and *B. inaequale*. Distinguished from *B. zephyrum* by characters mentioned under that species's account. As well, leftmost central membranes of internal sac with large, heavily sclerotized scales, unlike those found in *B. zephyrum*. From *B. inaequale* distinct in having the outer mirrors near the anterior silver spot; these outer mirrors are generally connected to the inner mirrors in *B. levettei*.

Description.– As in Table 2, plus: *Size*. SBL = 4.8-6.1mm. *Color*. Dorsal surface greenish-grey, aeneous, or bronze; mirrors purplish, reddish, or coppery; silver spots greenish-grey, aeneous, or bronze. Appendages dark, piceous except extreme base of legs and (in a few specimens only) venter of antennomere 1 rufous. *Microsculpture*. Pronotum with distinctly contrasted shiny discal band near midline present or faint; with a small "silver spot" near the lateral edge of this band. *Thorax*. Sides of pronotum moderately sinuate. *Elytron*. Humeral margin short, not extended to interneur 5; interneurs slightly to moderately impressed. *Female genitalia*. Spermatheca varied; with very long cornu, slightly to distinctly curved. basal portion short (Fig. 177). Spermathecal duct without posterior lobe.

Stylomeres as in Figs. 160-161; no consistent differences observed between the subspecies.

First instar larva (Fig. 231)

Diagnostic combination.– As for *B. lorquinii*. *Size.*– LHw = 380-420 µm, LHl = 315-355 µm, LCl/LHl = .137-.155. Six specimens measured. See Table 2 for complete description.

Second instar larva (Fig. 218)

Description.– As for *B. lorquinii*. LHw = 580-625 µm (n=2).

Specimens examined.– I have seen 1606 adults, 36 first instars, 9 second instars, and 1 third instar from the following collections: AMNH, AMor, BJCa, BMNH, CAS, CNC, CUIC, DHKa, DRMa, FMNH, GDND, HNHM, ICCM, ISAs, JKLi, KUSM, MCZ, OSUO, ROM, SMNH, UASM, UBC, UMSP, UMMZ, USNM, ZIL.

Geographic distribution.– From Newfoundland and Labrador south in the east to New York, west to British Columbia, south to Colorado and northernmost New Mexico, and north to Alaska and N.W.T. (Fig. 272).

Geographic variation.– This variable species consists of two distinct forms, which I treat as subspecies, *B. levettei levettei* and *B. levettei carrianum*. The two forms are, as far as known, allopatric, with no signs of intergradation (although intermediate localities have not been well collected). One form is strictly southern and montane, and the other almost exclusively more northern or lowland (Fig.

272). The only exceptions I have seen are three specimens from Fort Collins, Colorado (CAS!). Two of these males have genitalia of the *B. levettei carrianum* form, and yet they are within the range of *B. levettei levettei*, far from the range of *B. levettei carrianum*. The third male is genitally intermediate between the two subspecies. The significance of these three specimens is uncertain; more material is needed from northern Colorado.

4.4.14.1 *Bembidion levettei levettei* Casey

Adult

Comparison with *B. levettei carrianum*.- Clearly distinguished from *B. levettei carrianum* only by male genitalia: members of *B. levettei levettei* lack the basodorsal lobe of the internal sac possessed by members of *B. levettei carrianum* (compare Fig. 125 with 124) (46 specimens of *B. levettei levettei* examined, 66 of *B. levettei carrianum*). In inverted internal sacs, this lobe of *B. levettei carrianum* is manifest as a characteristic bulge of the anterior edge of the ostial cavity (Fig. 103, arrow). *B. levettei levettei* aedeagi are generally larger, more curved ventrally, with a wider apex, but there are exceptions to these characters. However, there are a few somewhat consistent differences in external characters. Members of *B. levettei levettei* tend to be larger and shinier than *B. levettei carrianum*, with the mirrors more contrasted in luster and color to the surrounding surface.

This includes not only the mirrors of the elytra, but also the shiny areas of the pronotum, which are generally a shiny purplish contrasted against the dull greyish green of the rest of the pronotum. Mirrors on elytral intervals 5 through 7 tend to be a bit more extensive, and are positioned slightly more posteriad (compare Fig. 20 with 21). The interneurs of *B. levettei levettei* are a bit deeper (at least in northern populations). The elytra are slightly more parallel-sided, and relatively larger than the pronotum; the sides of the pronotum are less rounded (Fig. 20). Interneur 4 is more frequently straight in *B. levettei levettei*. Most of these external characters are rather vague, and none consistently distinguish the two subspecies.

Geographic distribution.– Found in the western mountains, from southern British Columbia and southwestern Alberta to Idaho, Wyoming, Colorado, and northernmost New Mexico (Fig. 272). I have seen as well one specimen from Washington, and another labelled "Cal." (MCZ).

4.4.14.2 *Bembidion levettei carrianum* Casey

Derivation of subspecific epithet.– Patronym honoring F.S. Carr.

Adult

Comparison with *B. levettei levettei*.– Very similar to *B. levettei levettei*; for a discussion of differences, see account of that subspecies.

Geographic distribution.– Transamerican, from Newfoundland and Labrador west through Minnesota to central Alberta, British Columbia, and north into Alaska and N.W.T.

Habitat.– *B. levettei* members are found most commonly on barren sand or sand-silt banks of rivers; also on creek and lake banks.

Phylogenetic relationships.– The relationships within the *B. inaequale*-subgroup are unclear (Fig. 278); indeed, I am not certain that the two subspecies of *B. levettei* are themselves sister taxa.

4.4.15 *Bembidion inaequale* Say

Bembidium inæqualis Say, 1823a:151. NEOTYPE male designated by Lindroth and Freitag (1969:335), examined, in MCZ, labeled: "Mt Pleasant Ia Apr 28 1934 Knutson / inaequale det. Darlington / Neotypus Bembidium inaequale Say design Lth [red label, in Lindroth's handwriting] / Bembidion inaequale Say s.str. det. Lindroth 68". Type locality Mount Pleasant, Iowa.

Bembidium arenarium Dejean, 1831:80. TYPE, examined by Lindroth (1962:7), in MNP. Type locality: "Amérique septentrionale".

Bembidium lacustre LeConte, 1848:451. HOLOTYPE female, examined, in MCZ. Labeled: " [greyish-green circle] / 428 / Type 5491 [red label] / var. lacustre Lec. [hand-written] / Bembidion inaequale Say Det Lindroth 1951". Type locality Lake Superior, according to Lindroth (1962:7).

Bembidion opaciceps Casey, 1918:8. LECTOTYPE female designated by Lindroth 1975:115, examined, in USNM. Labeled: "Cal. / CASEY bequest 1925 / TYPE USNM 36794 [red label] / opaciceps Csy [hand written] / LECTOTYPE opaciceps Csy By C.H. Lindroth". Type locality California.

Derivation of specific epithet.– From the Latin "*inaequalis*", referring to the "unequal surface" of the elytra.

Adult (Figs. 22, 23, 73, 74, 126, 142, 162, 178)

Diagnostic combination.– Mirrors present on intervals 2 through 7; outer mirrors on intervals 6 and 7 near posterior silver spots, frequently isolated from inner mirrors (Figs. 22-23); pronotum with carina short or absent, midlateral seta present or absent; aedeagus with prominent ventral bulge and hooked apex (Fig. 126); extensive dorsal field of comb-like scales; VSP scaly, as in *B. levettei*.

Comparisons with related species.– Adults are generally smaller than those of *B. levettei*, from which they differ externally by small silver spots, and the mirror on elytral intervals 6 and 7 being positioned near the posterior silver spot. Generally the outer mirror is a small spot, isolated from the inner mirrors, but in many specimens it is broadly connected to inner mirrors. Eastern members of *B. inaequale* are more readily distinguished from *B. levettei* specimens by the narrow forebody with deeply punctured interneurs, and pale tibia.

Description.– As in Table 2, plus: *Size.* SBL = 4.3-5.9mm. *Color.* Dorsal surface ranging from dark bronze or dark aeneous to grey green, aeneous, or bluish green; mirrors dark purplish black, dark bronze, or coppery, or reddish. Antenna with first four antennomeres pale, at least basally, or more generally infuscated; tibia centrally pale, rufous or rufotestaceous with slight metallic tint; femora basally pale; western specimens with more generally infuscated legs. *Microsculpture.* Faint discal shiny patch flanked by dull patches on pronotum. *Thorax.* Pronotum varied, from convex and narrow to flat and wide. *Elytron.* Transverse basal impression of elytra not as pronounced as in *B. levettei*, in many specimens absent; humeral margin short to medium in length, not extended to interneur 5; interneurs slightly to markedly punctate; 5 and 6 in many specimens interrupted at outer mirror; 4 in many specimens interrupted. *Female genitalia.* Spermatheca quite varied;

cornu slightly curved, length varied, as short as in Fig. 179 or nearly as long as in *B. levettei* (Fig. 177). Spermathecal duct without posterior lobe. Stylomeres as in Fig. 162.

First instar larva (Fig. 193)

Diagnostic combination.– As for *B. lorquinii*. *Size*.– LHw = 330-400 µm, LHl = 260-340 µm, LCl/LHl = .111-.161. Four specimens measured. See Table 2 for complete description.

Second instar larva

Description.– As for *B. lorquinii*.

Specimens examined.– I have seen 1802 adults, 62 first instars, 4 second instars, and 2 third instars from the following collections: AMNH, AMor, BJCa, BMNH, CAS, CNC, CUIC, DEUN, DHKa, DRMa, FMNH, GDND, HNHM, ICCM, ISAs, JHAc, JKLi, KUSM, MCZ, OSUO, ROM, SMNH, UASM, UBC, UCB, UMSP, UMMZ, USNM, UWLW, ZIL.

Geographic distribution.– In North America from Nova Scotia, south to Georgia and Alabama, west to Kansas, Colorado, and California, north to Alaska (Fig. 273).

Geographic variation.– This species shows considerable geographic variation. Lindroth (1963) divided *B. inaequale* into two subspecies, but I do not consider them discrete enough to be recognized.

Adults from east of the Great Plains ("*B. inaequale inaequale*", Fig. 22) are generally more somber in color, have paler legs, shinier luster, narrower body (especially the forebody), and deeper elytral punctures; they lack the midlateral pronotal seta. Specimens from the western mountains ("*B. inaequale opaciceps*", Fig. 23) are wider and more robust; the microsculpture is deeper, with surface therefore duller; pronotum wider with less sinuate sides and broader base; midlateral setae present in most specimens; interneurs much shallower, with less impressed punctures; shoulder margin a bit longer. The two forms are quite different.

However, there is a broad zone of intermediates, from Alberta and Manitoba south to Colorado, Wyoming, and Nebraska. Within this intergradation zone there is also notable variation, with Alberta and Saskatchewan specimens being: larger, more reddish, with smaller silver spots, restricted to interval 3; with mirrors more extensive, outer mirrors frequently not isolated.

Making the picture more complex are five specimens from Nampa, Idaho (ICCM!) which appear quite like intergrade specimens from western Nebraska, even though they are from well within the range of the western form.

I feel that a detailed morphometric study of the patterns of geographic variation in this species is necessary before any clear division into subspecies is undertaken.

Habitat.– Found on river, creek, and lake banks. Generally among sparse vegetation on a silt-sand substrate.

Phylogenetic relationships.– *B. inaequale* is either the sister species of *B. levettei levettei*, *B. levettei carrianum*, the *B. litorale*-*B. baikaloussuricum* line, or a combination thereof (Fig. 278).

4.4.16 *Bembidion litorale* (Olivier)

Elaphrus litoralis Olivier, 1790:6. Location of type unknown, according to Lindroth (1962:6). Type locality Paris, France.

Elaphrus paludosus Panzer, 1794, number 4. Location of type unknown. Type locality Nürnberg, Germany.

Bembidium elegans Germar, 1824:27. Location of type unkown. Type area Transsylvania.

Bembidium var. *caeruleum* Krynicki, 1832:85 (not Serville 1826:76). Type presumably in Krynicki collection, University of Charkow (Horn and Kahle 1937). Type locality undesignated. [Name available as original description does not give clear indication that the name is intended to be infrasubspecific.]

(*Bembicidium palmosum* var. *evanescens* Dalla Torre, 1877:53 (not Wollaston 1877:18). Presumably "*palmosum* Pnz". is an emendation of "*paludosum* Panzer". [Name unavailable as intended as infrasubspecific.])

(*Bembidium littorale* v. *nigrans* Barthe, 1912:234. [Name unavailable as infrasubspecific, as indicated by "Ça et là avec la type." (Barthe 1912:234).])

(*Bembidium litorale* ab. *melanoticum* Wagner, 1915:307. [Name unavailable as intended as infrasubspecific.])

(*Bembidion litorale* ab. *krynickii* Csiki, 1928:35; new name for *Bembidium* var. *coeruleum* Krynicki 1832. [Name not available, as Csiki considered it of infrasubspecific rank.])

B. littorale auctorum.

Derivation of specific epithet.– From the Latin "*litoralis*", meaning "of the shore", referring to the beachside habitat of these beetles.

Adult (Figs. 17, 56, 81, 127, 143, 163, 179)

Diagnostic combination.– Mirrors on intervals 2 through 7, outer mirrors broadly connected or isolated from inner mirrors; pronotum basally constricted (Fig. 17), somewhat convex, lacking carina, midlateral setae present or absent; male protarsomere adhesive setae narrow (as in Fig. 86); aedeagus stout (Fig. 127), with dorsally bent ventral margin of the ostial cavity; VSP large, with unscaled (but occasionally striated) dorsal ridge; ostial microtrichal patch narrow, dense.

Comparisons with related species.– Males of this species have exceptionally thin basal protarsomeres, with small adhesive setae, traits they share with members of the closely related *B. baikaloussuricum*. *B. litorale* has a more convex prothorax with more rounded sides (that is, much more basally constricted) than does *B. baikaloussuricum*. Other differences from *B. baikaloussuricum* are described under that species.

Both Netolitzky (1940, 1942) and Lindroth (1962) considered the eastern populations of *B. litorale*-like *Chrysobracteon* to belong to a separate species, *B. baikaloussuricum*. O.L. Kryzhanovskij (pers. comm. 1983) suggests that *B. baikaloussuricum* and *B. litorale* belong to the same polytypic species. I have decided to treat the forms as distinct species, in good part because the limited material before me prevents a definitive conclusion (and thus I would prefer to err on the side of conservancy), but also because of the nature of the geographic variation. The few (11) specimens I have from a zone of sympatry, the Lena River, belong to two forms. Two females (Ust Kut, UMHF!) with convex, rounded prothorax, possessing midlateral setae, ed3 and ed5 in center of silver spots, and outer mirrors isolated, are typical *B. litorale* members. Nine specimens (Ust Aldan, Aldan, Ust Kut, Ust Vilui, UMHF!) have flatter, less rounded prothoraces, lack midlateral setae, have ed3 and ed5 at or near the anterior edge of silver spots, and the outer mirrors broadly connected to the inner mirrors or partly isolated, are more similar to typical *B. baikaloussuricum*. However, most of the characters Lindroth (1962) uses to separate the species are inconstant (especially the isolation of the outer mirrors), and the differences between the forms are rather slight. Kryzhanovskij's suggestion of synonymy of the two names thus deserves greater attention than I have been able to give it; an examination of geographic variation of *B. litorale*-like *Chrysobracteon* based on more extensive material is warranted.

Description.– As in Table 2, plus: *Size.* SBL = 5.2-5.9mm. *Color.* Dorsal surface bronze grey, bronze, or greenish grey; mirrors dark bronze grey, or purplish. Appendages dark, with venter of antennomere 1, base of legs, and venter of tibiae paler (rufous or rufopiceous). *Microsculpture.* Deeply microsculptured, and therefore quite dull. Shinier specimens show a slight silver spot on the prothorax. *Thorax.* Convex pronotum, sides distinctly rounded, greatest width well before middle; base narrow. *Elytron.* Humeral margin short, not extended to interneur 5; interneurs slightly to moderately impressed. *Female genitalia.* Spermatheca as in Fig. 179; cornu straight, basal bulb small. Spermathecal duct without posterior lobe. Stylomeres as in Fig. 163.

First instar larva

Unknown.

Second and third instar larvae

Diagnostic combination.– Described by Andersen (1966); he does not provide information on the characters I studied.

Specimens examined.– I have seen 241 adults from the following collections: AMNH, BMNH, CAS, HNHM, ICCM, MCZ, UMHF, USNM, ZMLS.

Geographic distribution.– A Palearctic species, found from the British Isles and Spain, to Greece, north to Finland, and east across Asia to the Lena River (Lindroth 1962; Fig. 274).

Geographic variation.– None noted.

Habitat.– On banks of rivers and small lakes, on fine sand often mixed with silt; bank often sparsely vegetated (Lindroth 1945). The habitat is thus similar to that of *B. inaequale*.

Phylogenetic relationships.– I have placed *B. litorale* as the sister species of *B. baikaloussuricum* (Fig. 278).

4.4.17 *Bembidion baikaloussuricum* Netolitzky

Bembidion baikalo-ussuricum Netolitzky, 1940:163 or 1942:54. HOLOTYPE male, examined by Lindroth (1962:7), in Naturh. Mus. Vienna. Type locality Nikolsk-Ussurisk, north of Vladivostok, U.S.S.R.

Bembidion baicaloussuricum auctorum.

Derivation of specific epithet.– From two of the localities of capture of members of this species, the Lake Baikal and Ussur regions of the Soviet Union.

Adult (Figs. 18, 86, 128, 144, 164)

Diagnostic combination.– Mirrors on intervals 2 through 7, outer mirrors broadly connected or isolated from inner mirrors; pronotum only slightly basally constricted (Fig. 18), relatively flat, generally with small carina, midlateral setae present or absent; male protarsomere adhesive setae narrow; aedeagus narrower than in *B. litorale*, with less curved ostial sclerotized strip (Fig. 128); VSP large, with unscaled (but occasionally striated) dorsal ridge; ostial microtrichal patch narrow, thick.

Comparisons with related species.– Very similar to specimens of *B. litorale*. The prothorax of *B. baikaloussuricum* is flatter, with straighter sides and a wider base than that of *B. litorale*; the midlateral seta is constantly absent in *B. baikaloussuricum*, only inconstantly so in *B. litorale*. A minute laterobasal carina is present in most *B. baikaloussuricum*, but in no *B. litorale*. The outer mirrors are broadly connected to the inner elytral mirrors in most, but not all, specimens. Interneur 4 is generally straighter (although in some specimens it is abruptly sinuate); ed3 and ed5 are at the anterior margin of the silver spot in most specimens. Aedeagus very similar to that of *B. litorale* (compare Figs. 127 and 128); slenderer, VSP usually thinner, with anterior basin shallower, ventral margin thus appearing straighter in side view; ostial cavity without markedly bent ventral margin.

Distinguished from the North American *B. levettei* by the lack of the prothoracic seta and the narrow protarsomere of the male.

Description.– As in Table 2, plus: *Size*. SBL = 5.3-5.7mm. *Female genitalia*. As in *B. litorale*; see Fig. 164.

First instar larva

Unknown.

Specimens examined.– I have seen 21 adults from the following collections: HNHM, UMHF, ZMLS.

Geographic distribution.– From the Lena River, Lake Baikal, and Mongolian Peoples' Republic, east to the Ussur region and Japan (Fig. 274; Lindroth 1962).

Geographic variation.– None noted.

Habitat.– Not known to me.

Phylogenetic relationships.– This species is probably most closely related to *B. litorale* (Fig. 278).

4.5 Species *incertae sedis*

4.5.1 *Bembidion uenoshiba* Jedlička

Bembidion uenoshiba Jedlička, 1965a: 94. HOLOTYPE female, in National Museum of Czechoslovakia, Prague, not examined. Type locality Uenoshiba (part of Osaka), Japan.

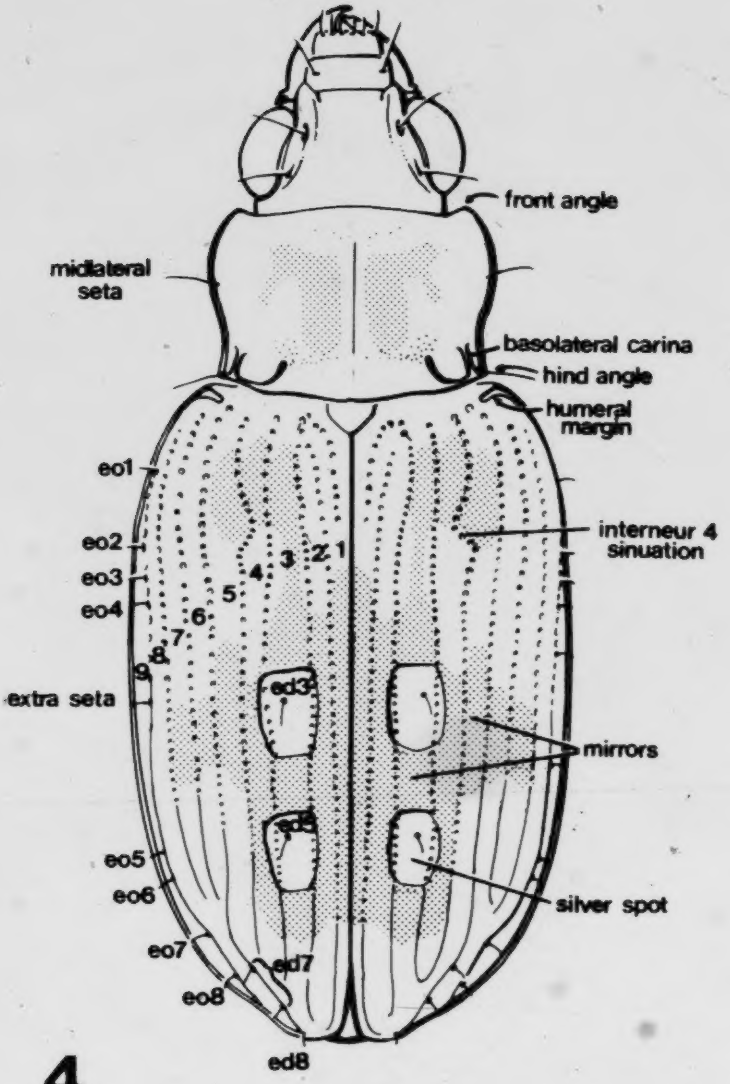
This name is not interpretable from the description. It may represent an otherwise unrecognized species, or may be a synonym of *B. argenteolum*, *B. alaskense*, or *B. lapponicum*, all of which could possibly occur in Japan.

Figure 4. Diagrammatic dorsal view of imaginary *Chrysobracteon* adult illustrating structures and terms.

Elytal setal codes (eo1, ed3, and so on) follow nomenclature of Erwin and Kavanaugh (1981). Note that in *Chrysobracteon*, there is either one or (as shown) two setae in the ed7 area.

Transverse basal impression of elytron is located at interneur 4 sinuation.

Elytral intervals are numbered.


front angle
midlateral seta
basolateral carina
hind angle
humeral margin
eo1
eo2
eo3
eo4
interneur 4 sinuation
1
2
3
4
5
6
7
8
9
extra seta
ed3
mirrors
ed5
eo5
eo6
silver spot
eo7
ed7
eo8
ed8

4

Figures 5 to 9. Dorsal view of adult male *Chrysobracteon*; appendages omitted. Scale bar=1mm.

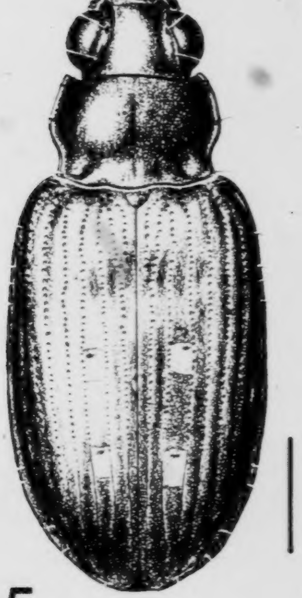
Figure 5. *B. balli* (Maymont, Saskatchewan).

Figure 6. *B. foveum* (Frenchman Butte, Saskatchewan).

Figure 7. *B. argenteolum* (Mora, Sweden).

Figure 8. *B. alaskense* (Lake Brooks, Alaska).

Figure 9. *B. semenovi* (Black Irtysh R., U.S.S.R.)



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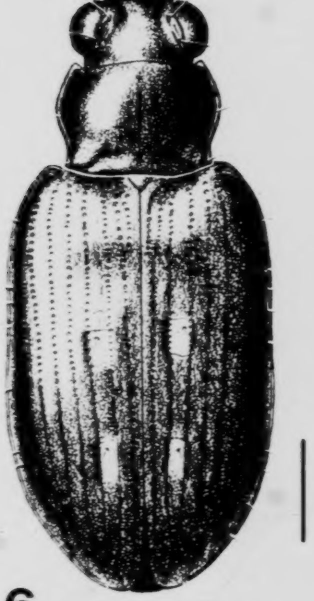

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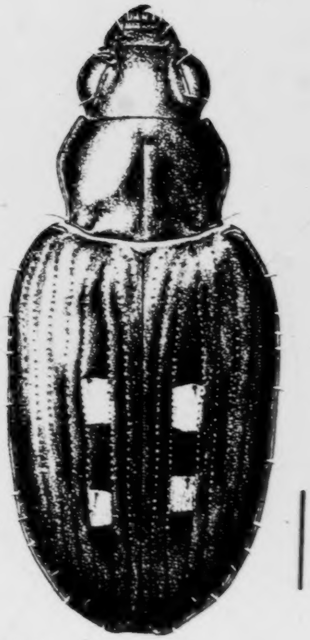

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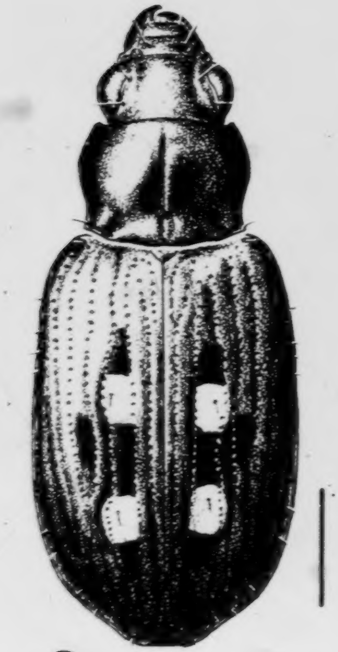

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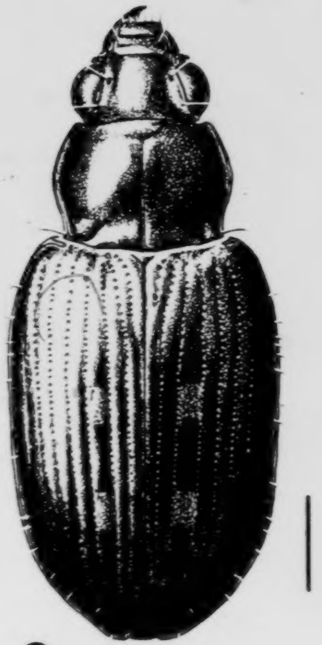


9

Figures 10 to 14. Dorsal view of adult male *Chrysobracteon*; appendages omitted. Scale bar=1mm.

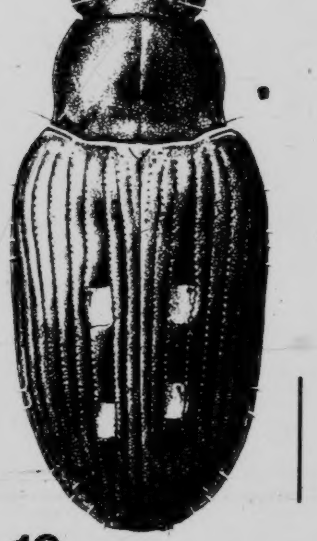
Figure 10. *B. stenoderum* (Kyoto, Japan).

Figure 11. *B. punctatostriatum* (Spring Creek Basin, Alberta).

Figure 12. *B. carinula* (North Saskatchewan River north of Lloydminster, Saskatchewan).

Figure 13. *B. velox* (Irtysh R., U.S.S.R.).

Figure 14. *B. lapponicum* (Old Crow, Yukon).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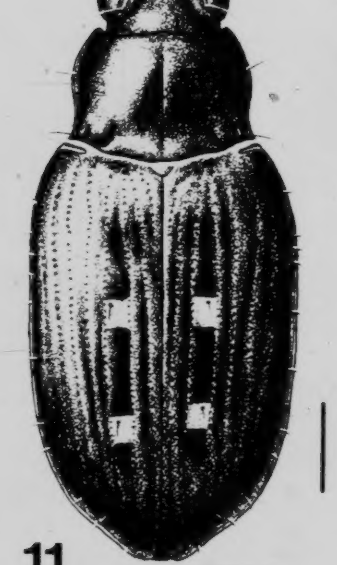
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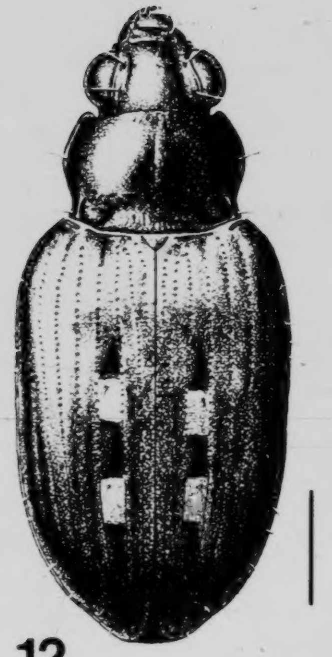
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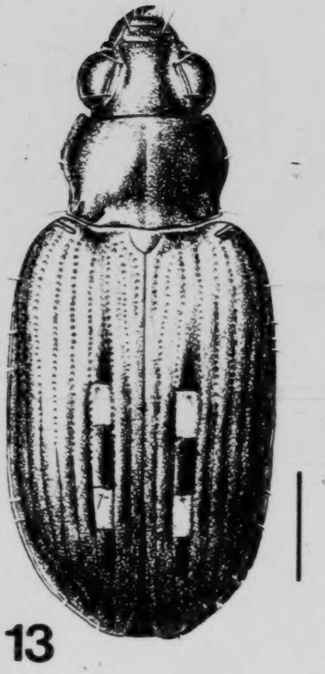
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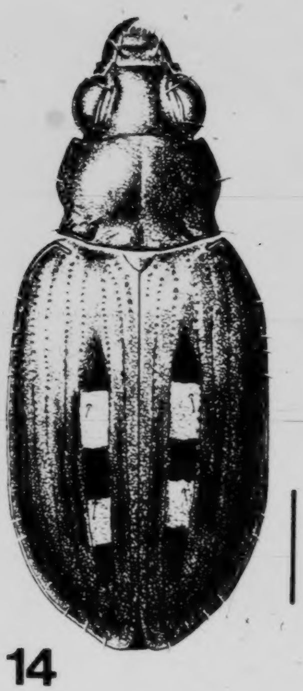

14

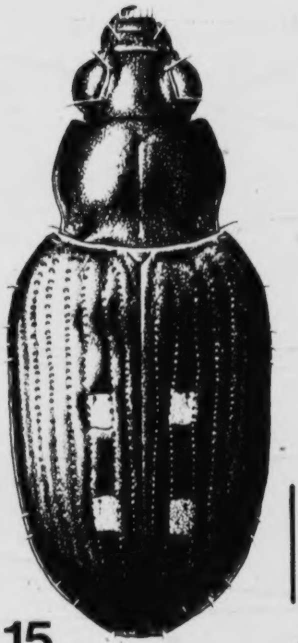
Figures 15 to 18. Dorsal view of adult male *Chrysobracteon*; appendages omitted. Scale bar=1mm.

Figure 15. *B. hesperium* (Van Zandt, Washington).

Figure 16. *B. lorquinii* (Lockwood, Nevada).

Figure 17. *B. litorale* (Emsdetten, Federal Republic of Germany).

Figure 18. *B. baikaloussuricum* (Ulan-Baator, Mongolian Peoples' Republic).



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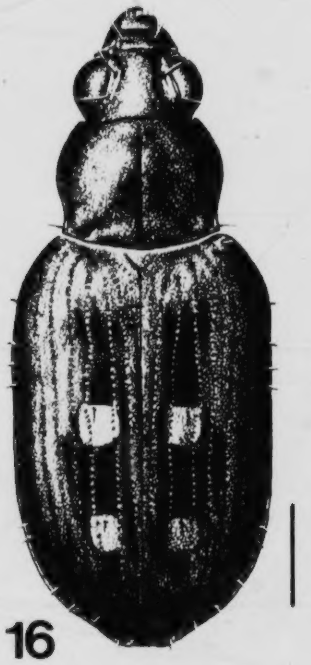

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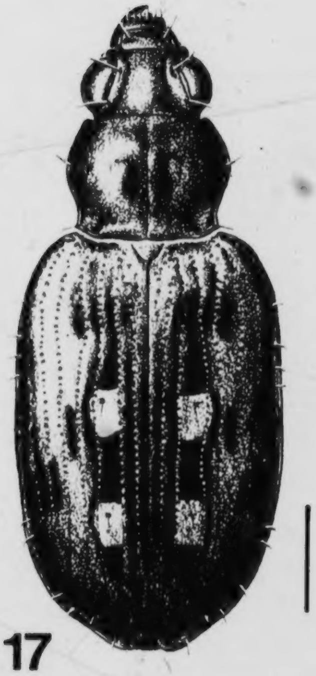

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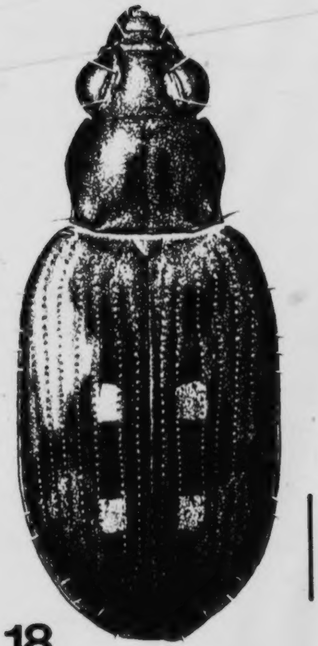

18

Figures 19 to 23. Dorsal view of adult male *Chrysobracteon*; appendages omitted. Scale bar=1mm.

Figure 19. *B. zephyrum* (Waldport, Oregon).

Figure 20. *B. levettei levettei* (Brocket, Alberta).

Figure 21. *B. levettei carrianum* (Paynton, Saskatchewan).

Figure 22. *B. inaequale* (Listowel, Ontario).

Figure 23. *B. inaequale* (Van Zandt, Washington).

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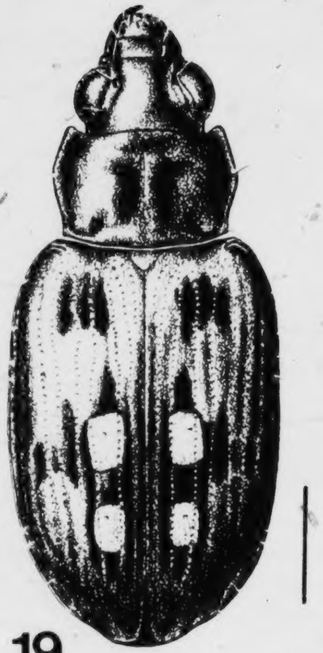

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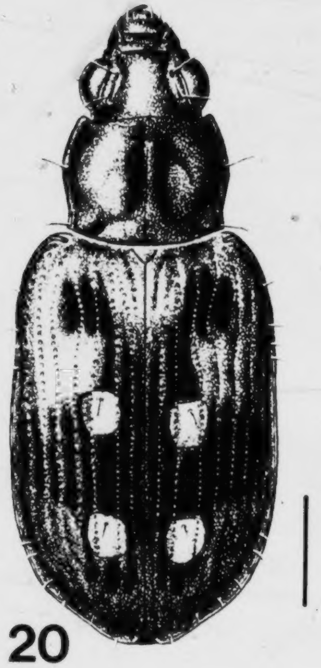

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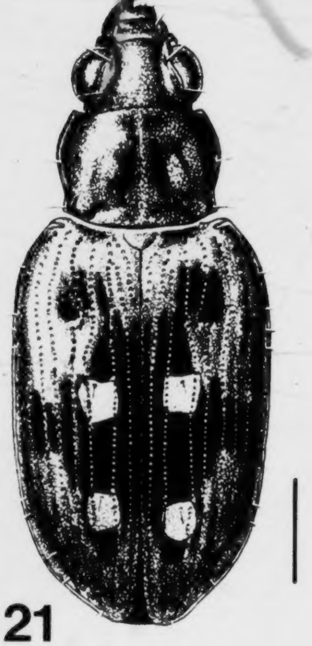

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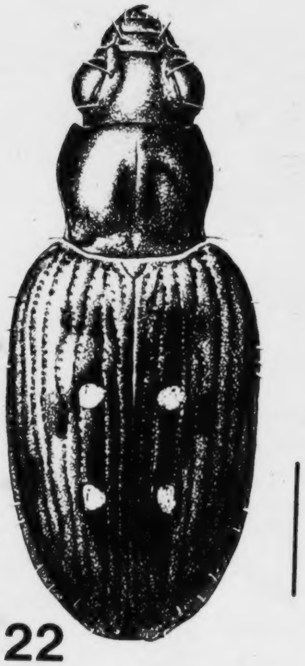

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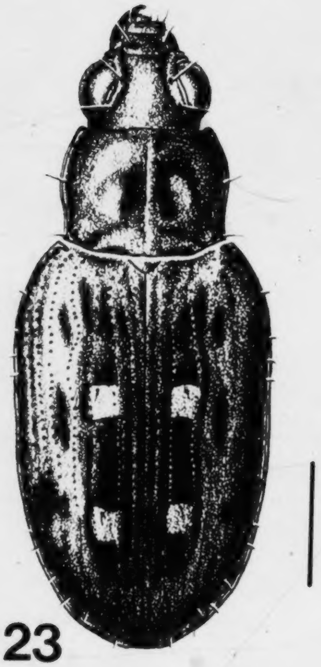


23

Figures 24 to 27. Cleared mouthpart structures of adult *B. foveum*. All figures at same scale; scale bar=100µm.

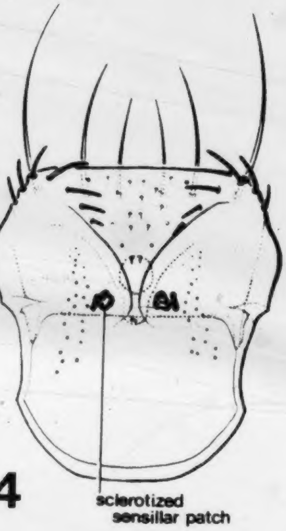
Figure 24. Ventral view of labrum.

Figure 25. Dorsal view of right mandible.

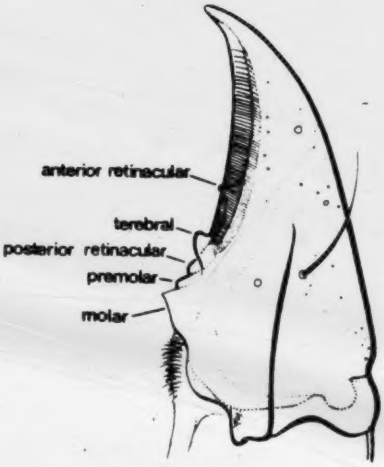
Figure 26. Ventral view of right maxilla.

Figure 27. Ventral view of mentum, ligula, and right labial palpus.

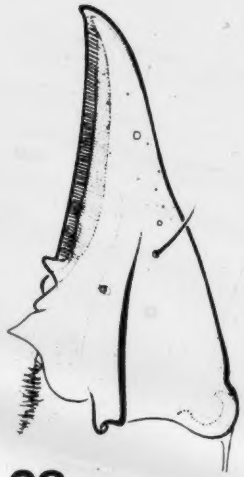
Figure 28. Dorsal view of cleared right mandible of *B. confusum*. Same scale as Figs. 24-27.


sclerotized
sensillar patch

24


anterior retinacular
terebral
posterior retinacular
premolar
molar

25



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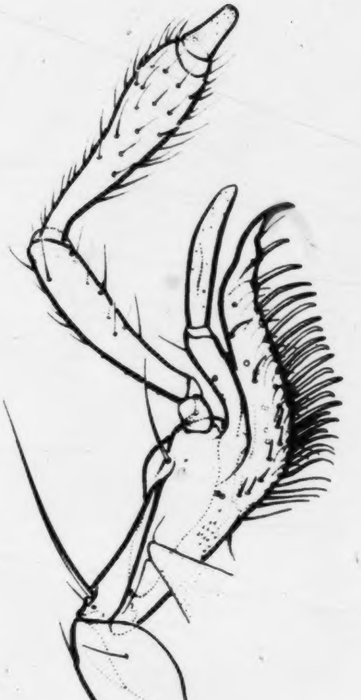

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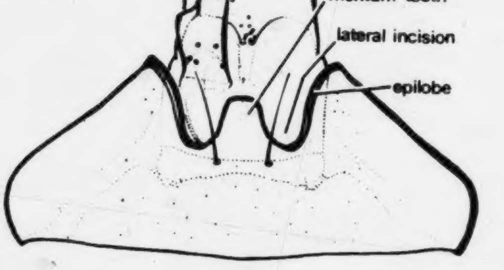

glossal
sclerite
paraglossal
lobe
mentum tooth
lateral incision
epilobe

27

Figures 29 to 36. Mandibles of *Chrysobracteon*.

Figure 29. Left mandible of *B. foveum*. Scale bar=200µm.

a. Dorsal view.

b. Mesal view.

c. Ventral view.

Figure 30. Right mandible of *B. foveum*. Same scale as Fig. 29.

a. Dorsal view.

b. Mesal view.

c. Ventral view.

Figure 31. Cleared right mandible of *B. foveum*, showing mesal pore canals. Scale bar=200µm.

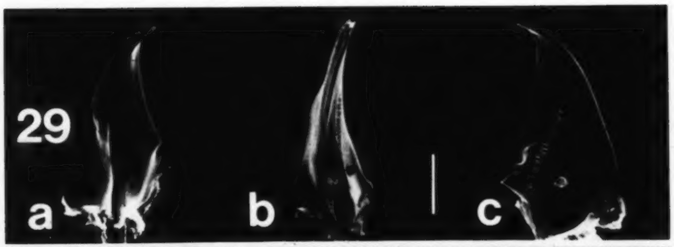
Figure 32. Basal mesal edge of right mandible of *B. foveum*, ventral view. Scale bar=40µm.

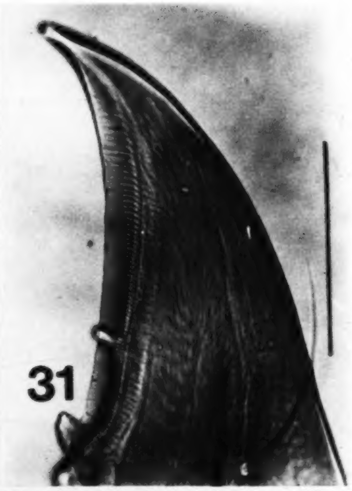
Figure 33. Basal mesal edge of right mandible of *B. punctatostriatum*, ventral view. Scale bar=40µm.

Figure 34. Microsculpture around terebral tooth of right mandible of *B. punctatostriatum*. Scale bar=10µm.

Figure 35. Dorsal surface of right mandible of *B. balli*, near dorsal condyle. Scale bar=40µm.

Figure 36. Dorsal surface of right mandible of *B. foveum*, near dorsal condyle. Scale bar=40µm.


29
a
b
c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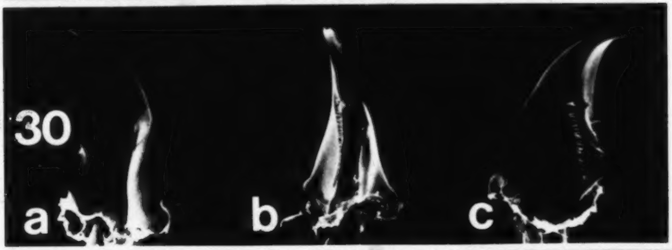
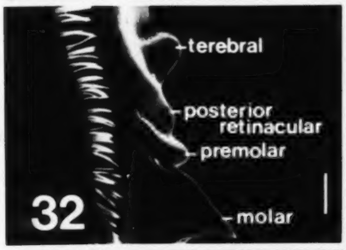
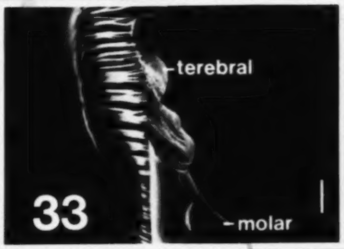
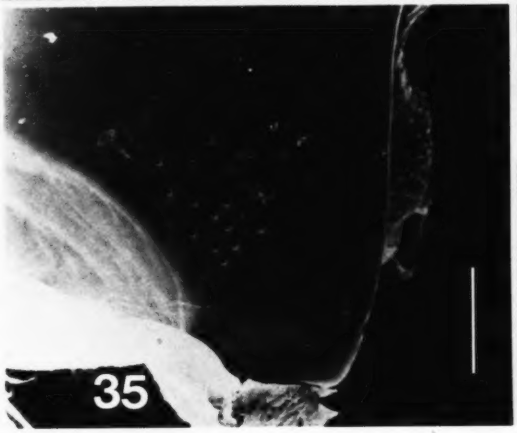

30
a
b
c


terebral
posterior retinacular
premolar
molar
32


terebral
molar
33

34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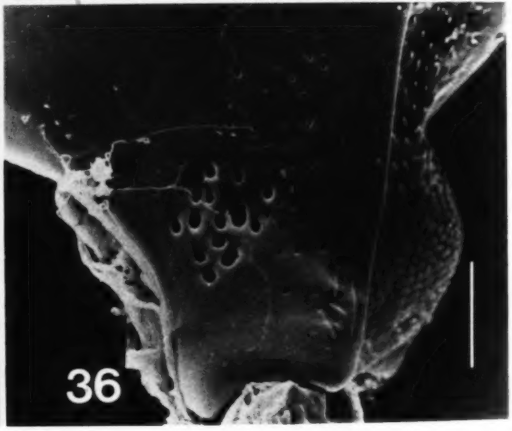

36

Figures 37 to 41. Mouthpart sensilla of adult *Chrysobracteon*. Scale bars=10µm.

Figure 37. Epipharynx of *B. foveum*, right side near epipharyngeal hump, ventral view.

Figure 38. Apex of maxillary palp of *B. foveum*.

Figure 39. Apex of labial palp of *B. foveum*.

Figure 40. Digitiform sensilla at base of maxillary palp of *B. balli*.

Figure 41. Apex of galea of *B. foveum*.

Figures 42 to 48. Right laciniae of *Bembidion*. Scale bars=100µm.

Figure 42. *B. confusum*, dorsal view.

Figure 43. *B. bowditchii*, dorsal view.

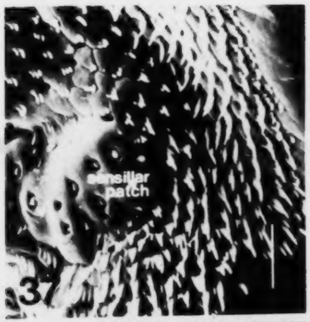
Figure 44. *B. lapponicum*, ventral view. Note subapical ridge (arrow).

Figure 45. *B. punctatostriatum*, ventral view.

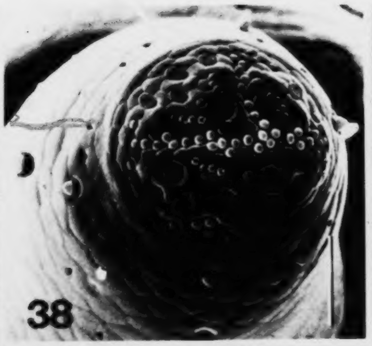
Figure 46. *B. lapponicum*, dorsal view.

Figure 47. *B. alaskense*, dorsal view.

Figure 48. *B. punctatostriatum*, dorsal view.


sensillar patch

37



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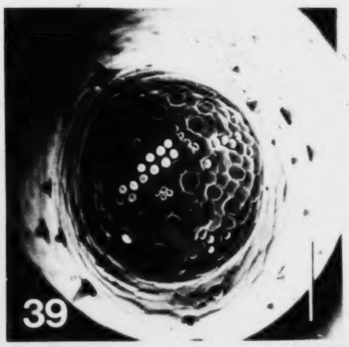

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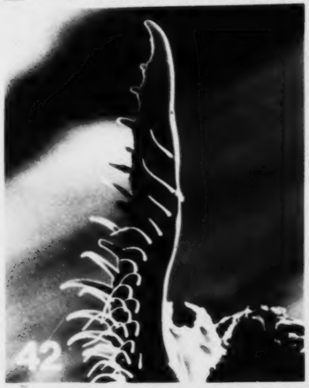

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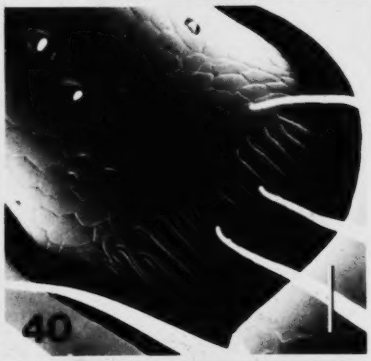

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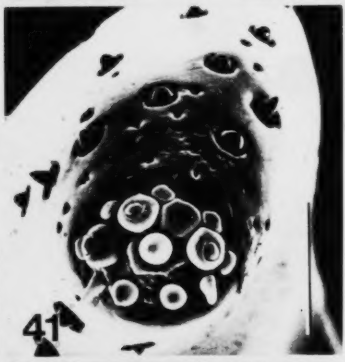

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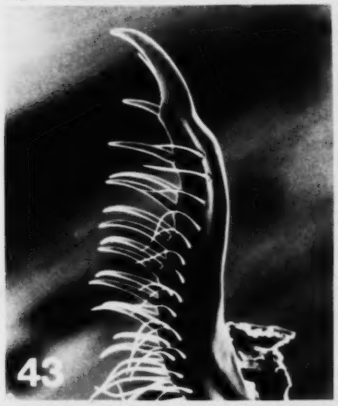

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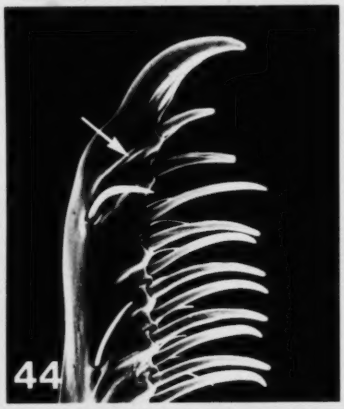

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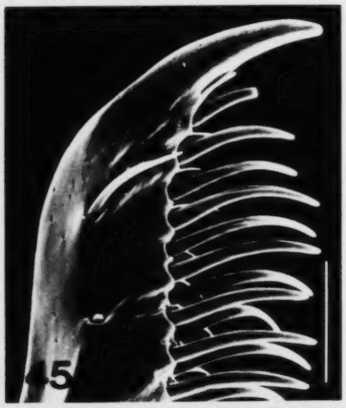

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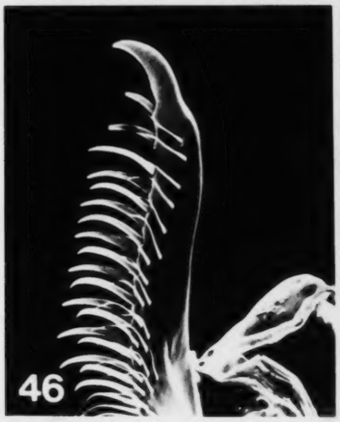

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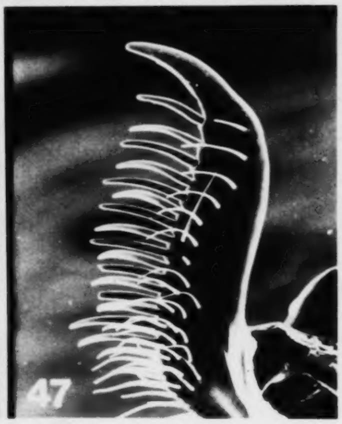

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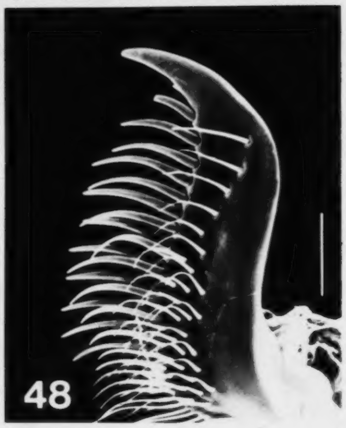


48

Figures 49 to 58. Menta of *Bembidion* adults, ventral view. Scale bar=200µm.

Figure 49. *B. balli.*

Figure 50. *B. alaskense.*

Figure 51. *B. lapponicum.*

Figure 52. *B. punctatostriatum.*

Figure 53. *B. hesperium.*

Figure 54. *B. zephyrum.*

Figure 55. *B. levettei carrianum.*

Figure 56. *B. litorale.*

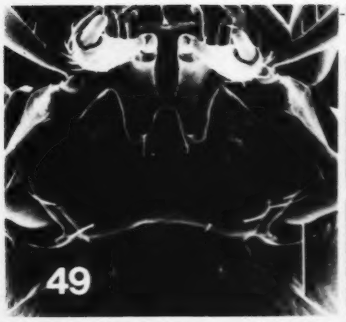
Figure 57. *B. cheyennense.*

Figure 58. *B. bifossulatum.*

Figures 59 to 60. Lateroventral views of *Chrysobracteon* heads. Scale bar=200µm.

Figure 59. *B. lapponicum.*

Figure 60. *B. punctatostriatum.*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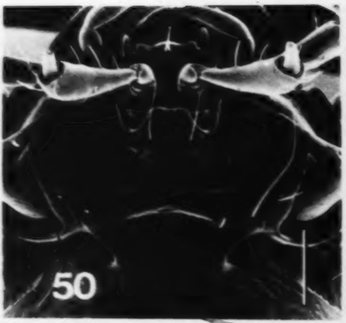
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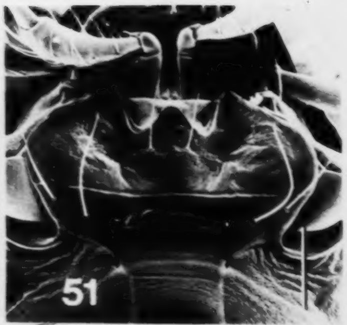
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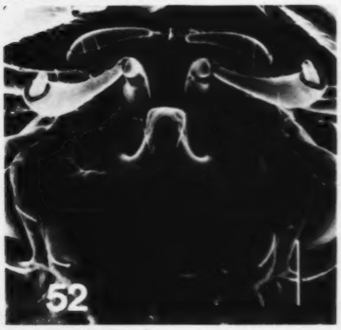
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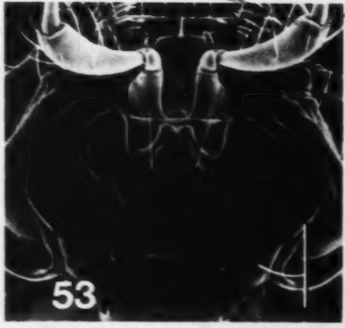
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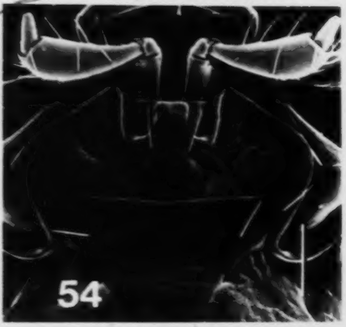
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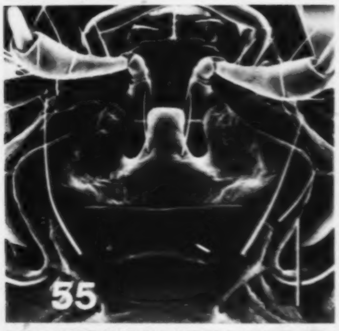
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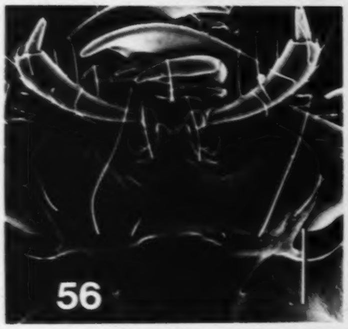
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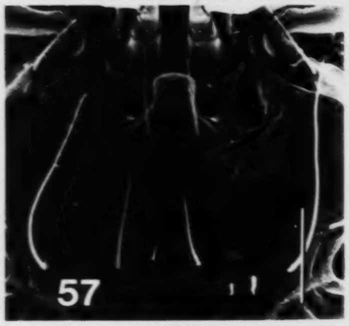
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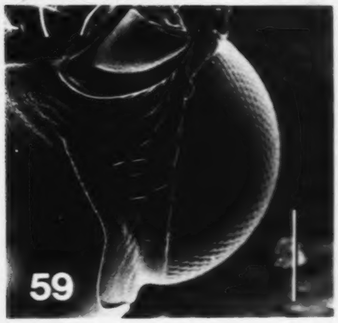
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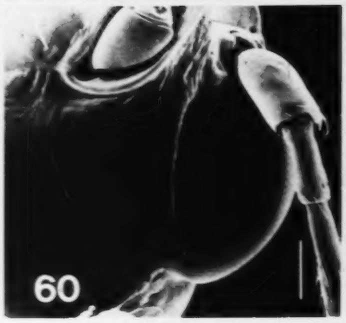
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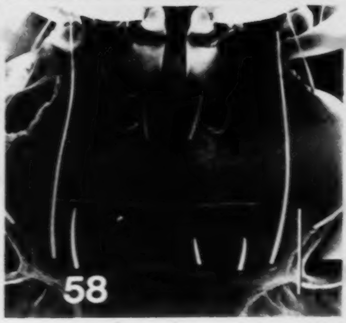

58

Figures 61 to 64. Elytral structure.

Figure 61. Right elytron, *B. lapponicum*, around seta ed3. Arrows indicate anterior and posterior limits of silver spot. Scale bar=200μm.

Figure 62. *B. balli*, microsculpture around seta ed3 in silver spot of elytron. Scale bar=40μm.

Figure 63. *B. foveum*, microsculpture around seta ed3 in silver spot of elytron. Scale bar=40μm.

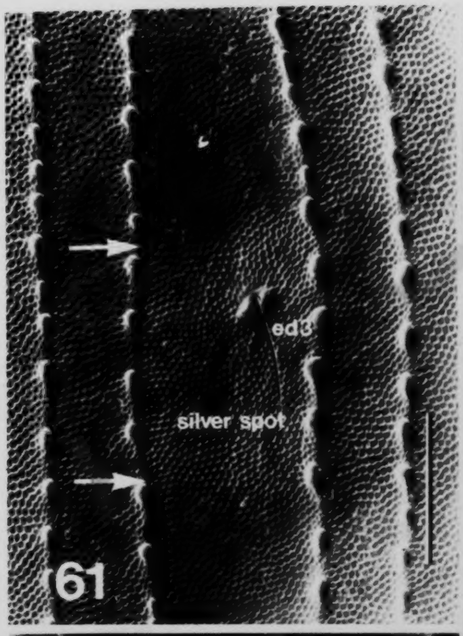
Figure 64. *B. hesperium* male, microsculpture of elytron in interval 6. Scale bar=40μm.

Figures 65 to 67. Ventral surface of elytral apex, showing subapical plica. Scale bars=200μm.

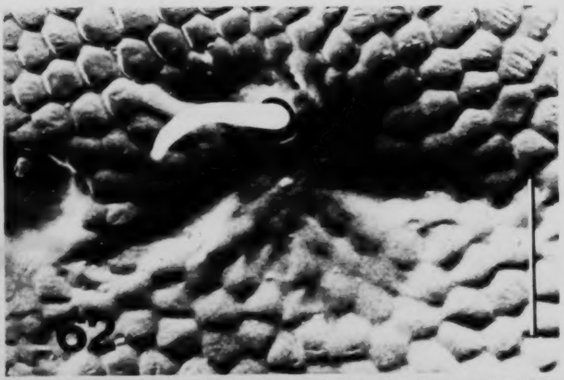
Figure 65. *B. aenulum.*

Figure 66. *B. confusum.*

Figure 67. *B. punctatostriatum.*


ed3
silver spot

61



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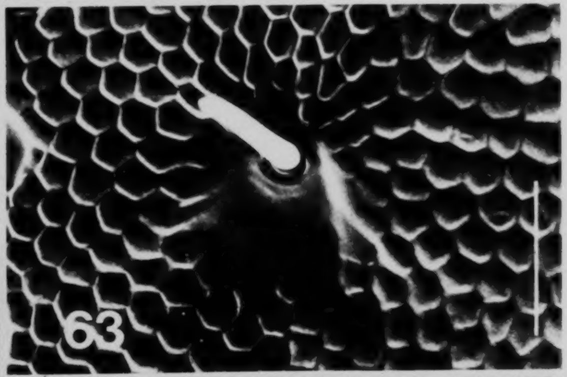

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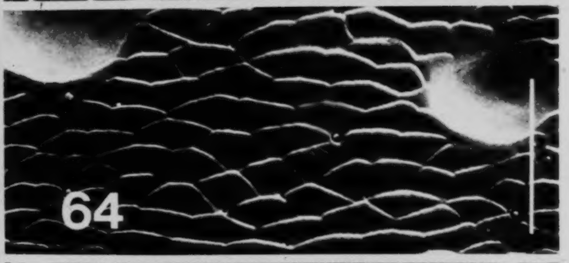

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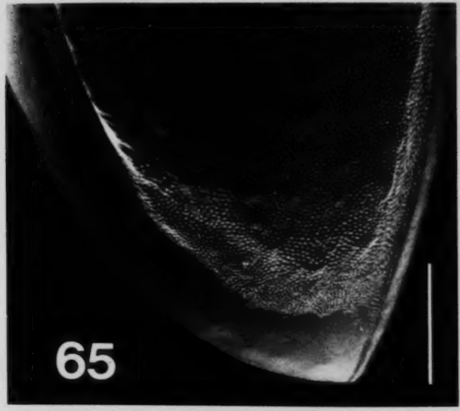

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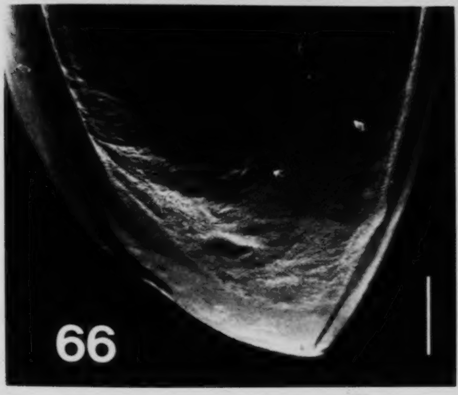

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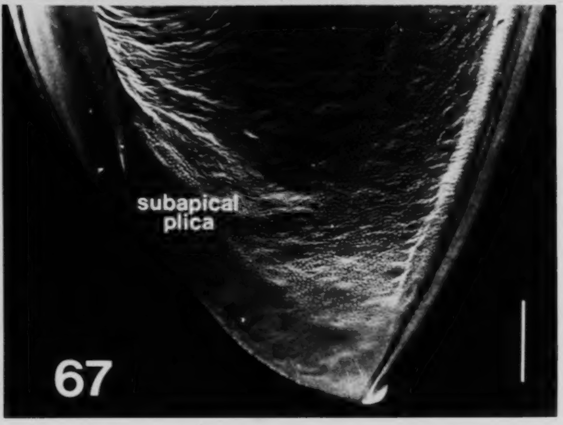

subapical
plica

67

Figures 68 to 73. Shoulder region of *Chrysobracteon*. Scale bar=.5mm.

Figure 68. *B. balli*.

Figure 69. *B. foveum*.

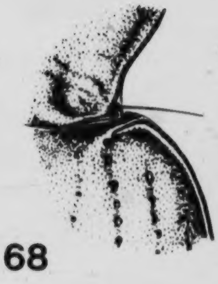
Figure 70. *B. carinula*.

Figure 71. *B. lapponicum*.

Figure 72. *B. punctatostriatum*.

Figure 73. *B. inaequale*.

Figure 74. Right metathoracic wing of *B. inaequale*. Scale bar=1mm.



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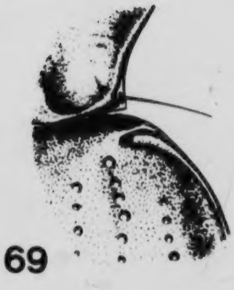

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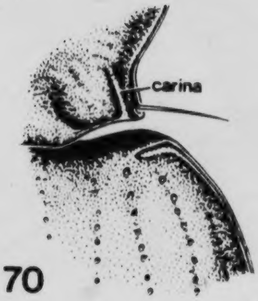

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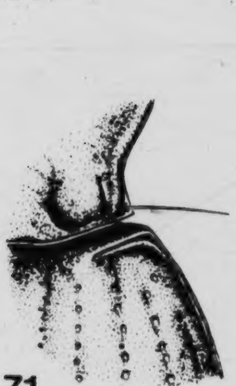

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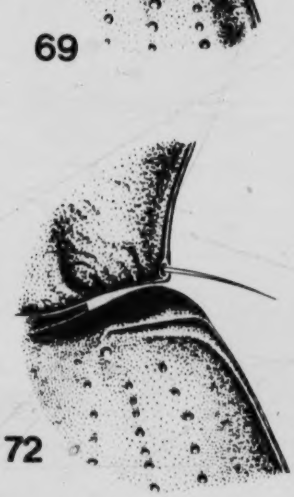

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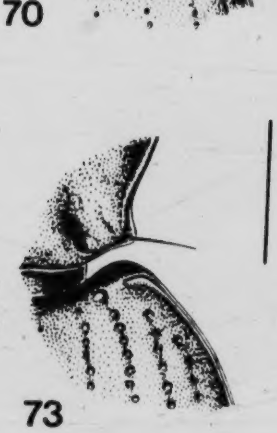
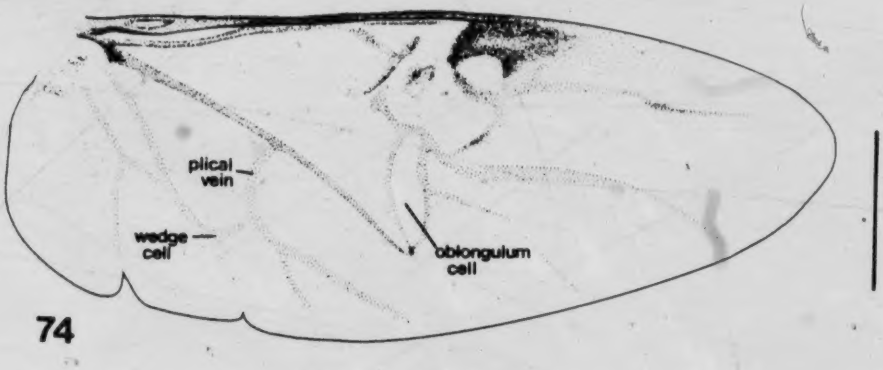


73


plical vein
wedge cell
oblongulum cell

74

Figures 75 to 81. First three male left protarsomeres of *Chrysobracteon*, dorsal view. Scale bar=100µm.

Figure 75. *B. balli.*

Figure 76. *B. foveum.*

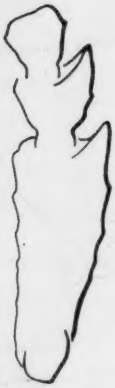
Figure 77. *B. argenteolum.* Note lack of lateroapical projection on protarsomere 3.

Figure 78. *B. semenovi.* Note lateroapical projection on protarsomere 3.

Figure 79. *B. zephyrum.*

Figure 80. *B. levettei levettei.*

Figure 81. *B. litorale.*



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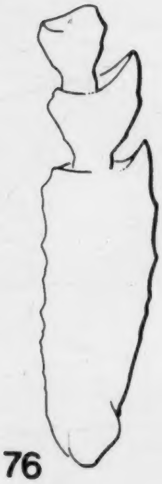

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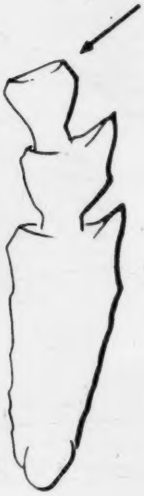

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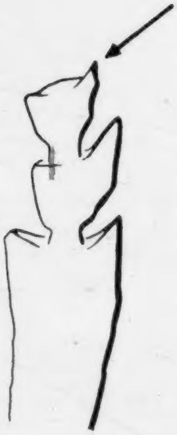

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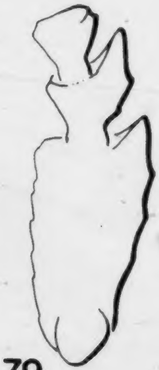

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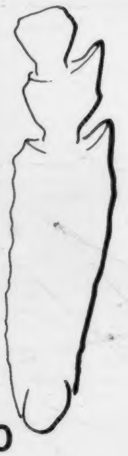

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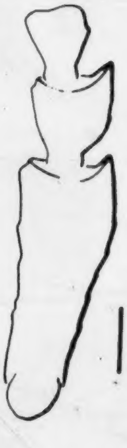


81

Figures 82 to 83. Lateral view of male protarsomere 1. Scale bar=100μm; Figs. 82 and 83 to same scale.

Figure 82. *B. zephyrum.*

Figure 83. *B. levettei levettei.*

Figures 84 to 87. Ventral view of male protarsus. Scale bar=100μm; Figs. 84-87 to same scale.

Figure 84. *B. zephyrum.*

Figure 85. *B. levettei carrianum.*

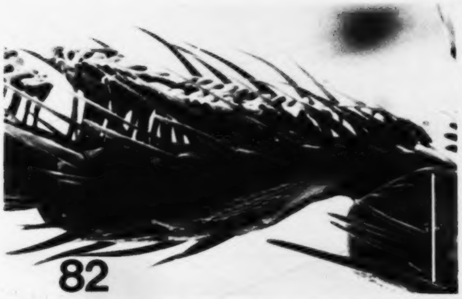
Figure 86. *B. baikaloussuricum.*

Figure 87. *Asaphidion alaskanum.*

Figures 88 to 89. Ventral view of male protarsomere 1, showing adhesive setae. Scale bars=20μm.

Figure 88. *B. argenteolum.*

Figure 89. *Asaphidion alaskanum.*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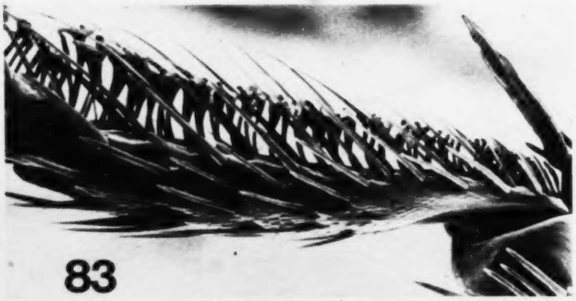
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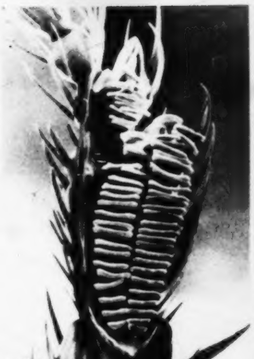
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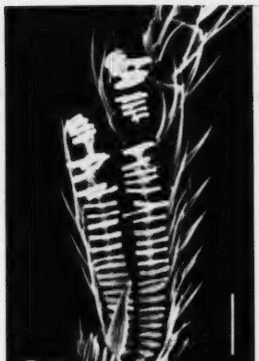
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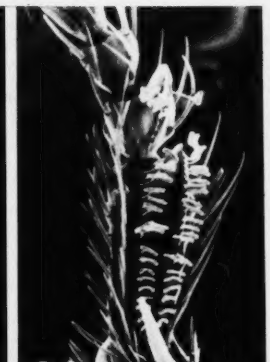
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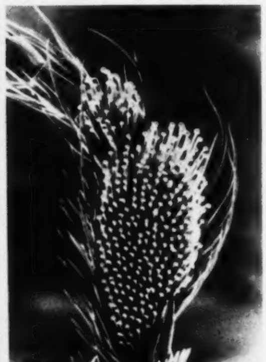
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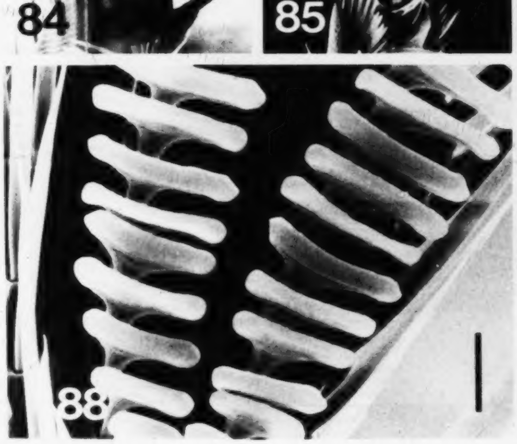
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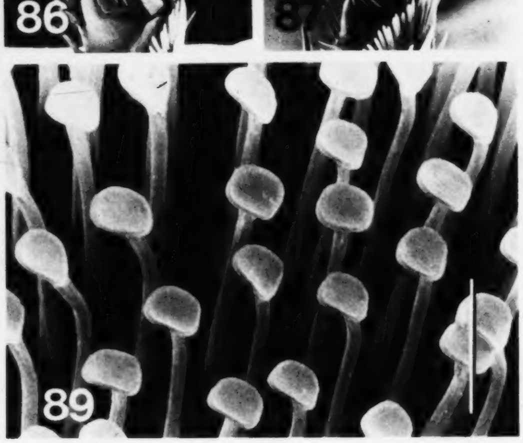

89

Figures 90 to 96. Ventral view of male protarsomeres.

a: protarsomeres 4 and 5; scale bars=100μm.

b: protarsomere 4; scale bars=40μm.

Figure 90. *Asaphidion alaskanum*.

Figure 91. *Bembidion interventor*.

Figure 92. *B. alaskense*.

Figure 93. *B. argenteolum*.

Figure 94. *B. punctatostriatum*.

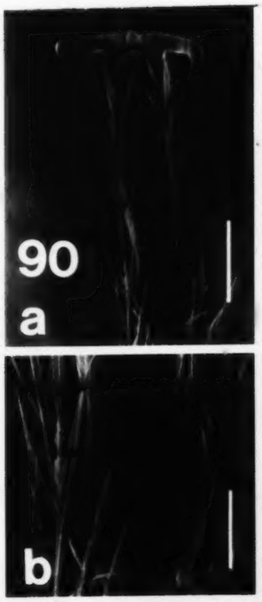
Figure 95. *B. hesperium*.

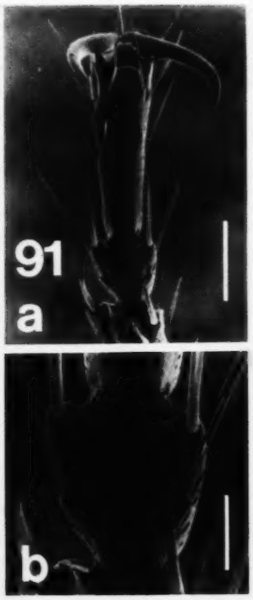
Figure 96. *B. balli*. fs: flattened ventroapical setae of protarsomere 4.

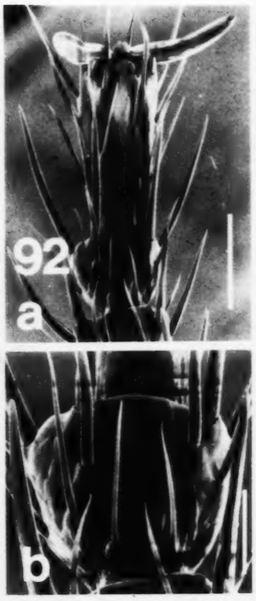
Figures 97 to 98. Lateral view of male protarsomere 4. Scale bars=40μm.

Figure 97. *B. argenteolum*.

Figure 98. *B. balli*. vap: ventroapical projection.


90
a
b


91
a
b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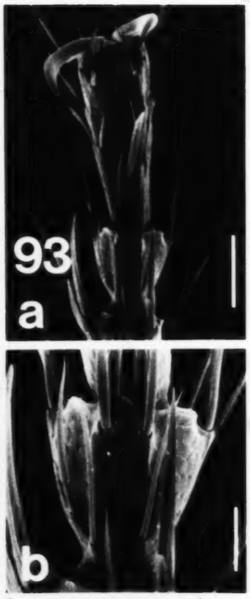
a
b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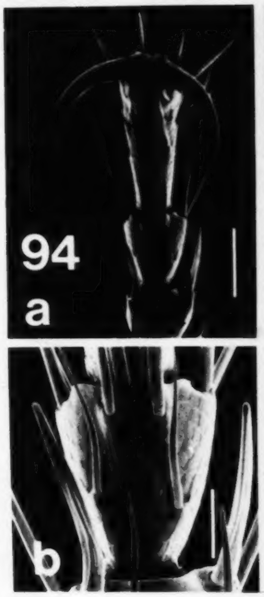
a
b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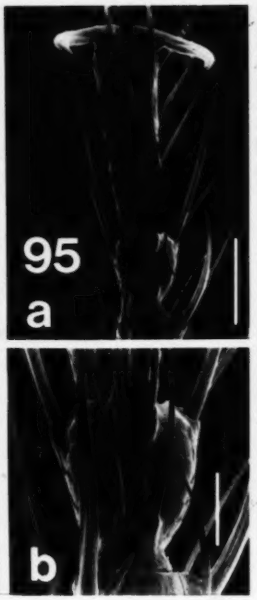
a
b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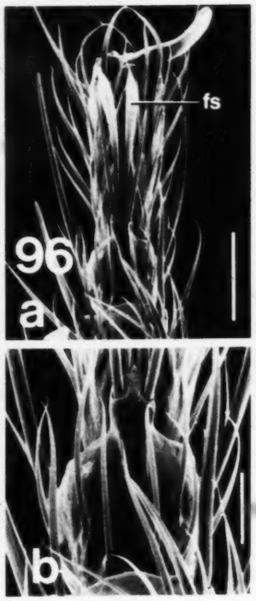
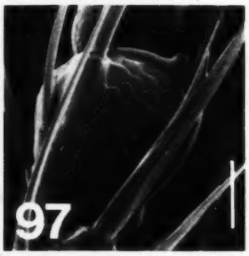
a
b


fs
96
a
b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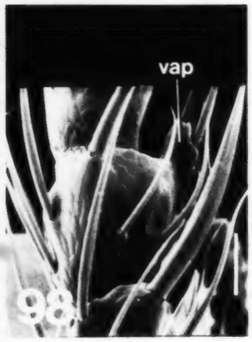

vap
98

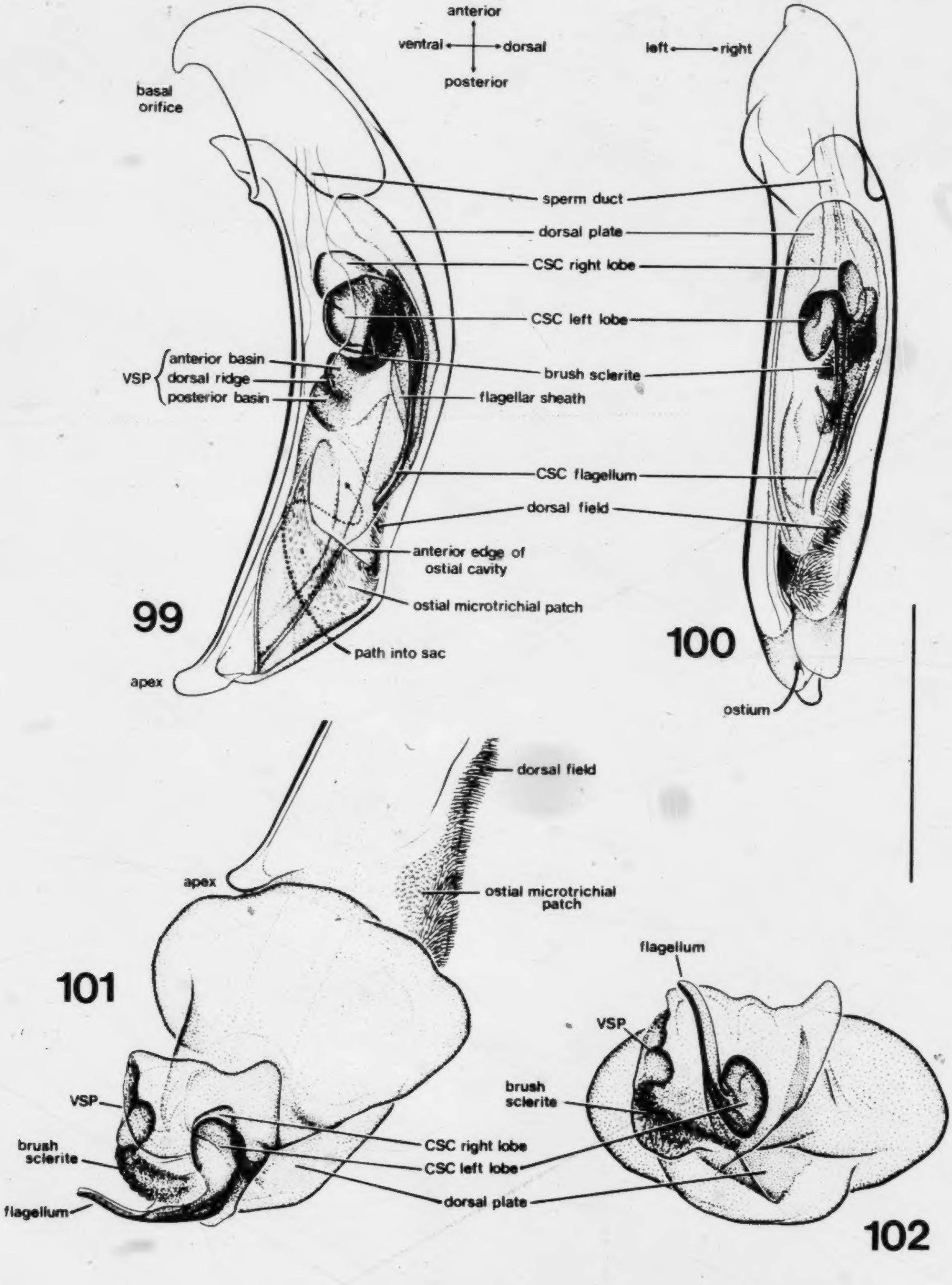
Figures 99 to 102. Median lobe of male aedeagus of *B. balli*; most membrane microsculpture omitted. Scale bar=.5mm.

Figure 99. Left lateral view of median lobe, internal sac inverted.

Figure 100. Dorsal view of median lobe, internal sac inverted.

Figure 101. Left lateral view of everted internal sac.

Figure 102. Apex of everted internal sac.


anterior
ventral
dorsal
posterior
left
right
basal orifice
sperm duct
dorsal plate
CSC right lobe
CSC left lobe
VSP
anterior basin
dorsal ridge
posterior basin
brush sclerite
flagellar sheath
CSC flagellum
dorsal field
anterior edge of ostial cavity
ostial microtrichial patch
path into sac
apex
ostium
99
100
dorsal field
apex
ostial microtrichial patch
101
flagellum
VSP
brush sclerite
VSP
brush sclerite
CSC right lobe
CSC left lobe
dorsal plate
flagellum
102

Figures 103 to 108. Internal sac microsculpture.

Figure 103. Everted internal sac of *B. levettei carrianum*, left lateral view. Arrow indicates basodorsal lobe. Scale bar=500µm.

Figure 104. Everted internal sac of *B. levettei carrianum*, microsculpture on left lateral face near ostial flag. Scale bar=50µm.

Figure 105. Everted internal sac of *B. levettei carrianum*, microsculpture on left lateral face. Scale bar=20µm.

Figure 106. Everted internal sac of *B. levettei carrianum*, microsculpture on right lateral face. Scale bar=20µm.

Figure 107. Everted internal sac of *B. cheyennense*, showing brush sclerite. Scale bar=20µm.

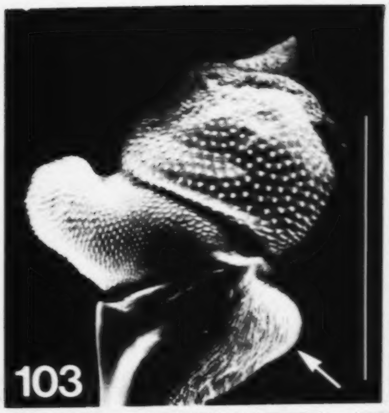
Figure 108. Everted internal sac of *B. chalceum*, showing large scales. Scale bar=20µm.

Figures 109 to 111. Left lateral view of flagella of *Chrysobracteon*. View slightly more ventral than in Figs. 129-144. Scale bars=40µm.

Figure 109. *B. balli*.

Figure 110. *B. alaskense*.

Figure 111. *B. levettei carrianum*.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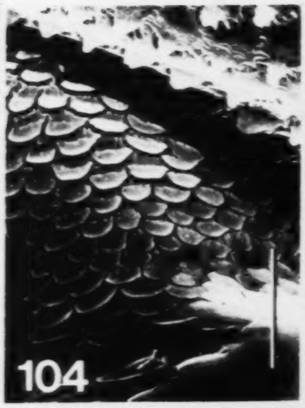
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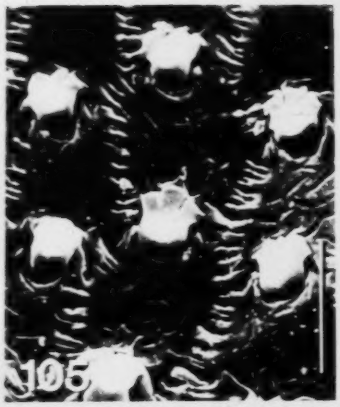
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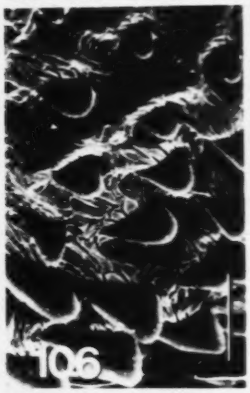
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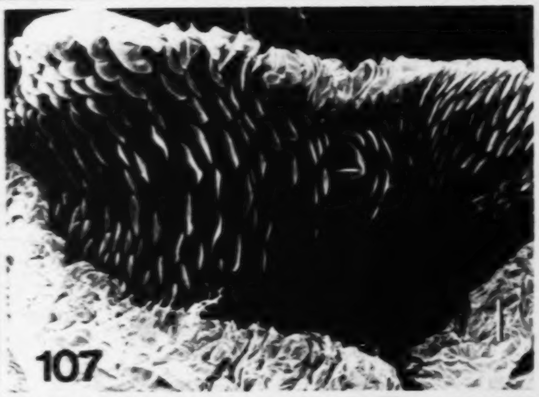
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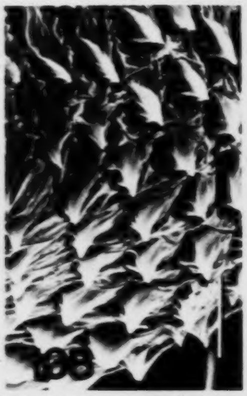
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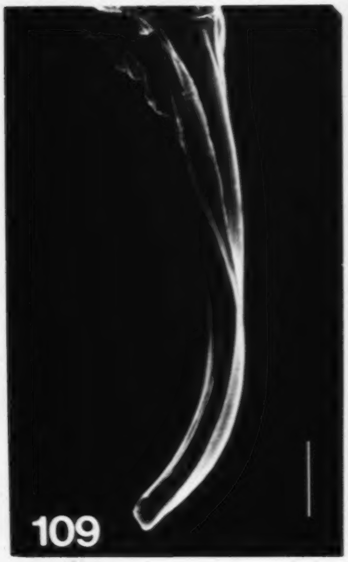
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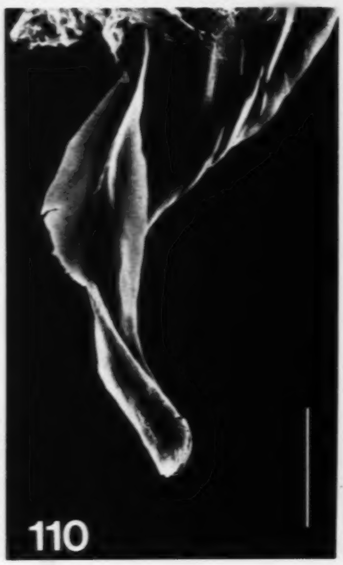
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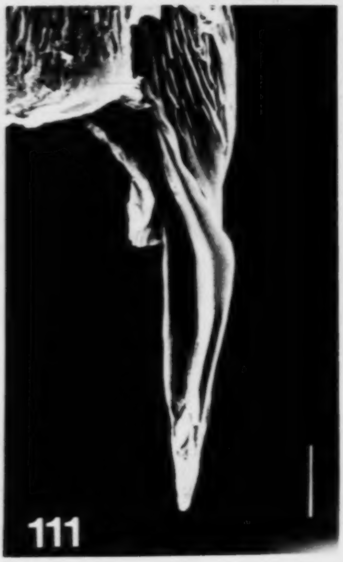

111

Figures 112 to 116. Median lobe of aedeagus, left lateral view. Scale bar=.5mm.

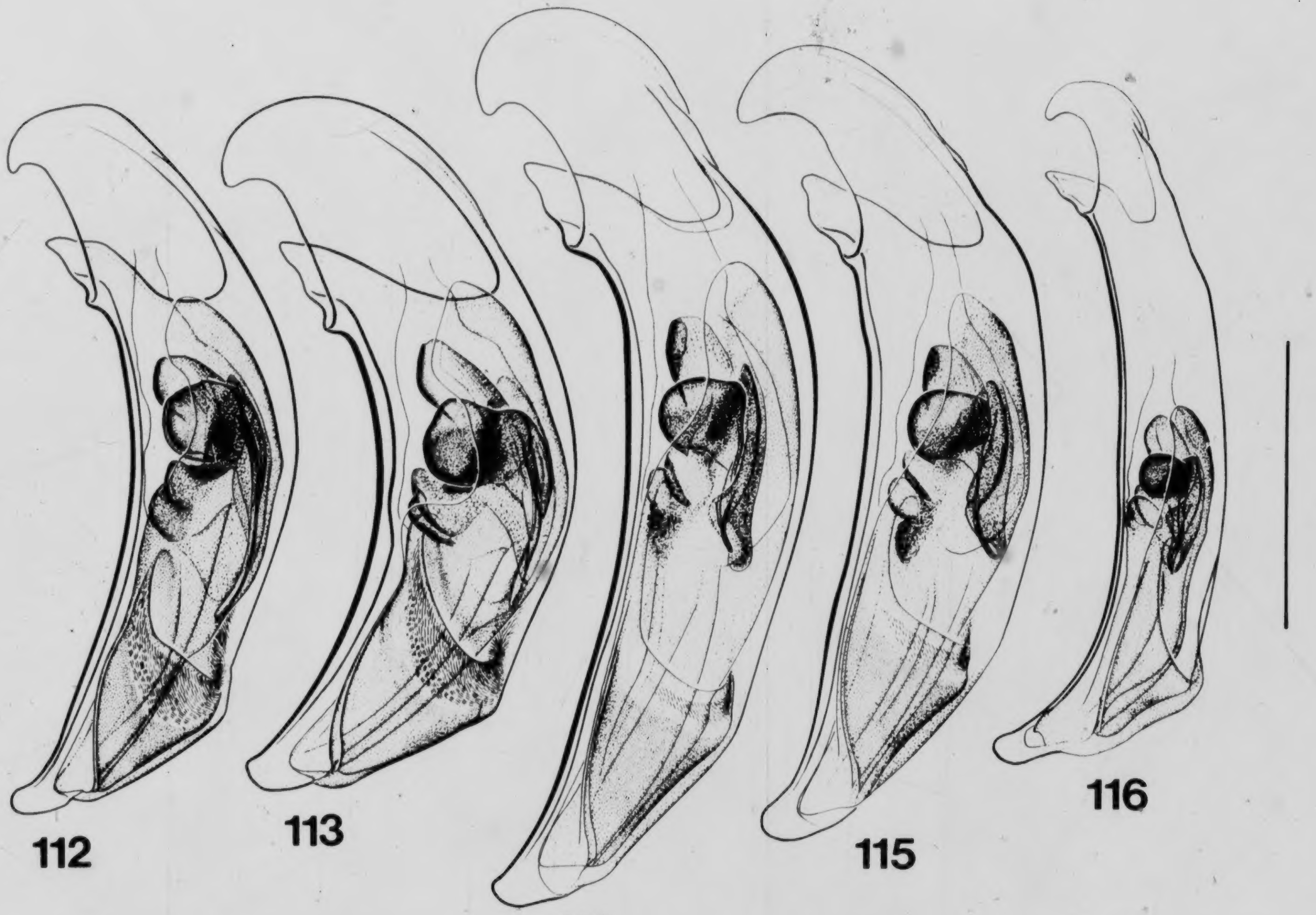
Figure 112. *B. balli.*

Figure 113. *B. foveum.*

Figure 114. *B. argenteolum.*

Figure 115. *B. alaskense.*

Figure 116. *B. stenoderum.*



Figures 117 to 122. Median lobe of aedeagus, left lateral view. Scale bar=.5mm.

Figure 117. *B. carinula.*

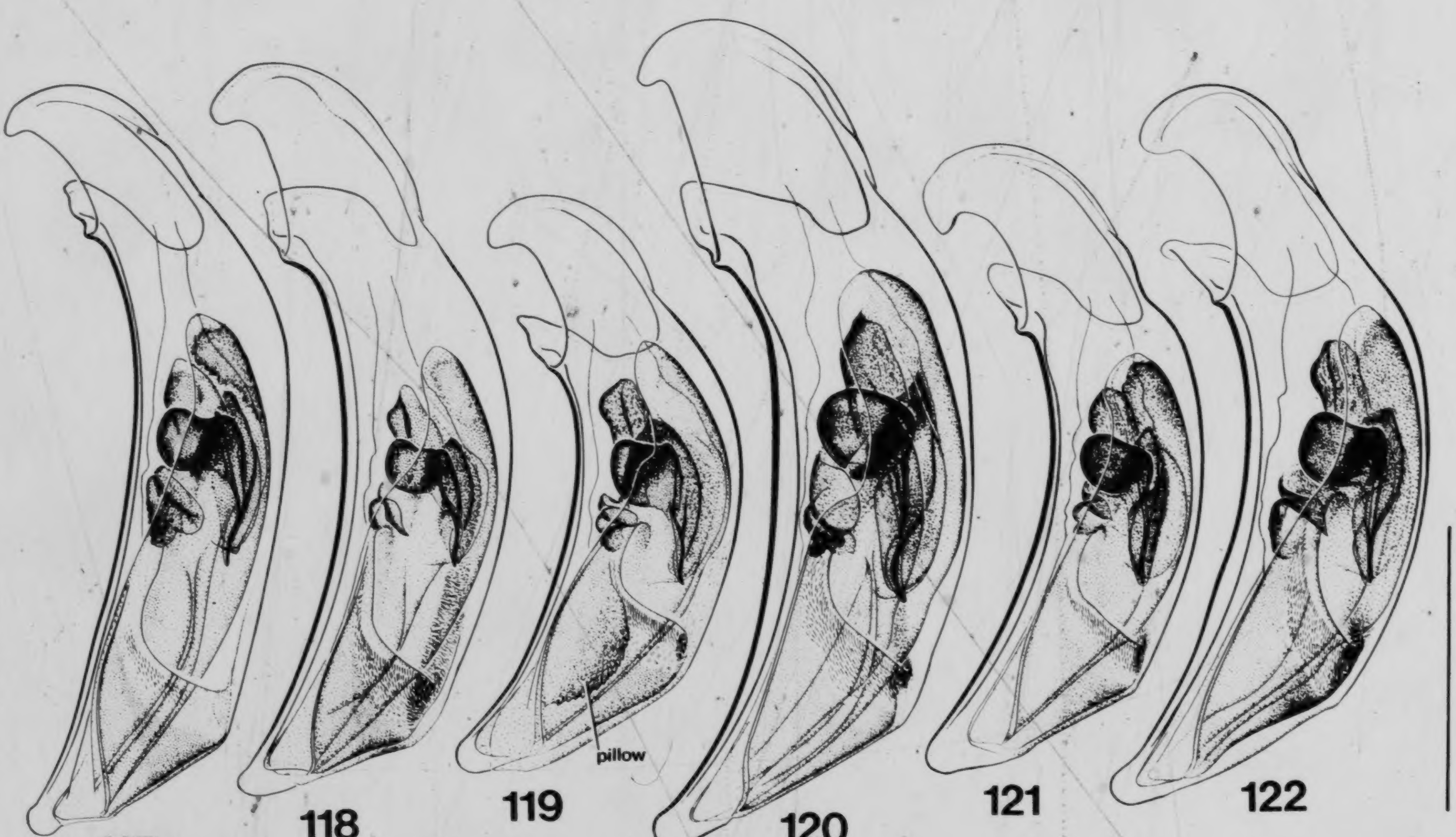
Figure 118. *B. velox.*

Figure 119. *B. lapponicum.*

Figure 120. *B. punctatostriatum.*

Figure 121. *B. hesperium.*

Figure 122. *B. lorquinii.*



117 118 119 120 121 122

Figures 123 to 128. Median lobe of aedeagus, left lateral view. Scale bar=.5mm.

Figure 123. *B. zephyrum*.

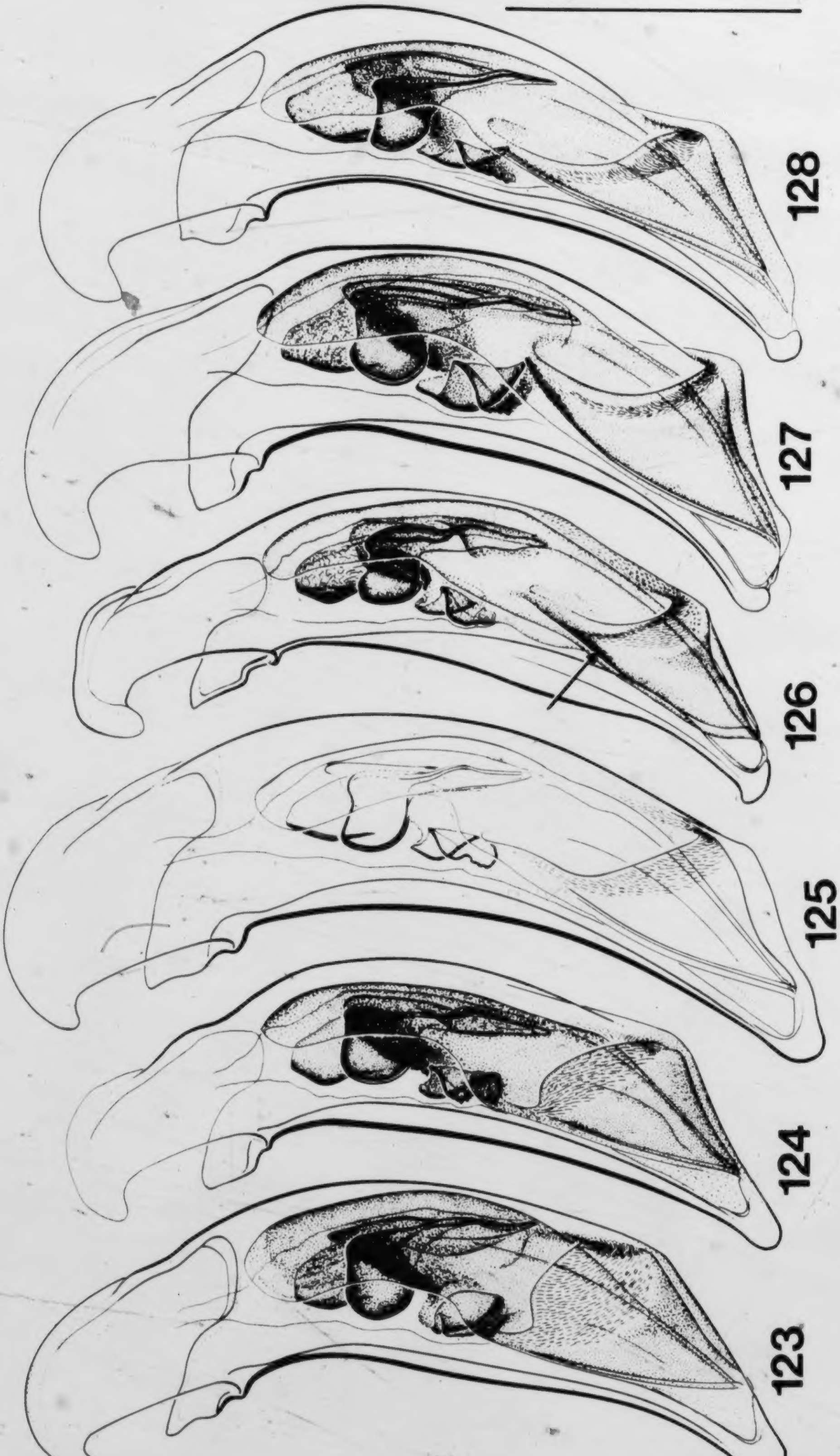
Figure 124. *B. levettei carrianum*.

Figure 125. *B. levettei levettei*.

Figure 126. *B. inaequale*. Arrow indicates position of ostial sclerotized strip.

Figure 127. *B. litorale*.

Figure 128. *B. baikaloussuricum*.



123

124

125

126

127

128

Figures 129 to 144. Central sclerite complex of male internal sac, with outline of brush sclerite, left lateral view. Scale bar=100μm.

Figure 129. *B. balli.*

Figure 130. *B. foveum.*

Figure 131. *B. argenteolum.*

Figure 132. *B. alaskense.*

Figure 133. *B. stenoderum.*

Figure 134. *B. carinula.*

Figure 135. *B. velox.*

Figure 136. *B. lapponicum.*

Figure 137. *B. punctatostriatum.*

Figure 138. *B. hesperium.*

Figure 139. *B. lorquinii.*

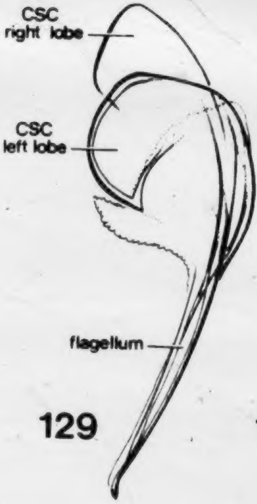
Figure 140. *B. zephyrum.*

Figure 141. *B. levettei carrianum.*

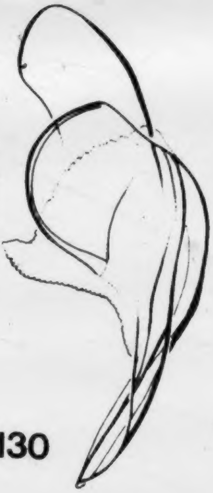
Figure 142. *B. inaequale.*

Figure 143. *B. litorale.*

Figure 144. *B. baikaloussuricum.*


CSC right lobe
CSC left lobe
flagellum

129



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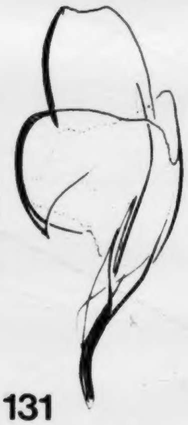

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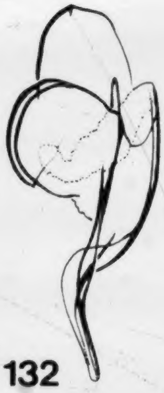

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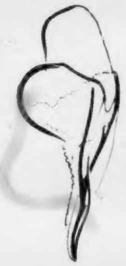

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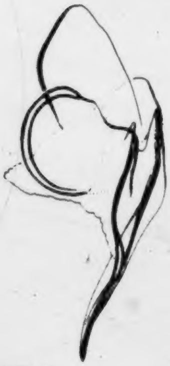

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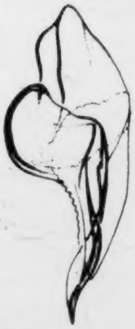

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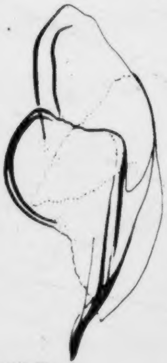

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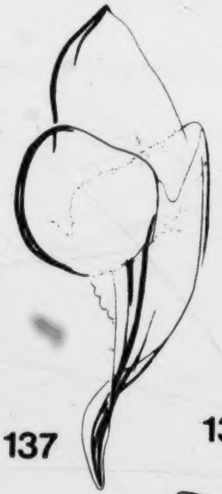

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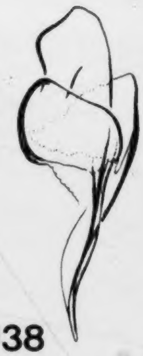

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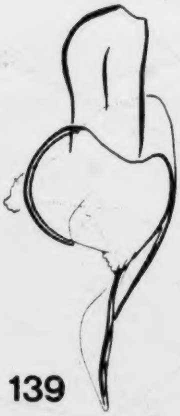

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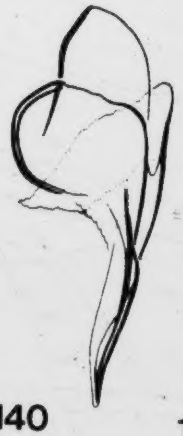

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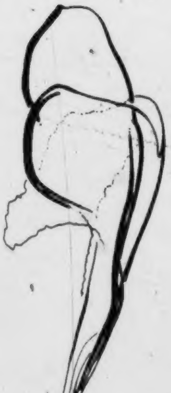

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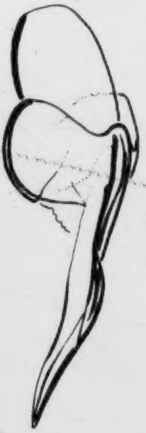

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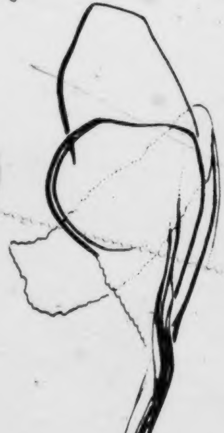

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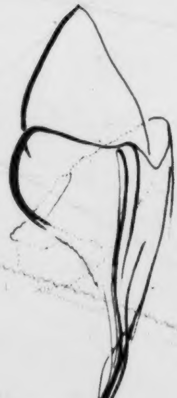


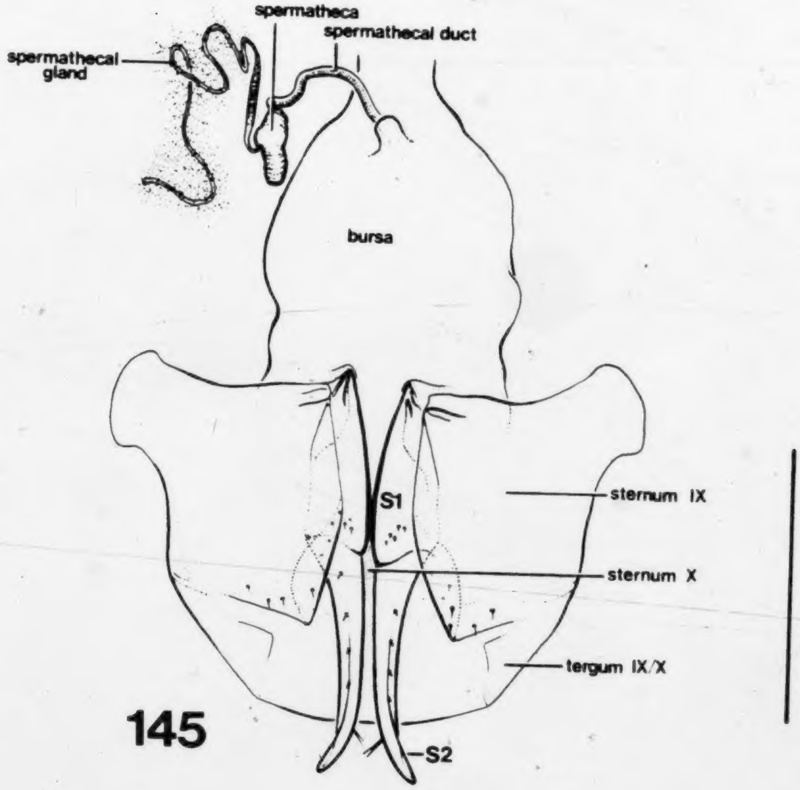
144

Figures 145 to 147. Ventral view of cleared, inverted female genitalia. Scale bar=.5mm.

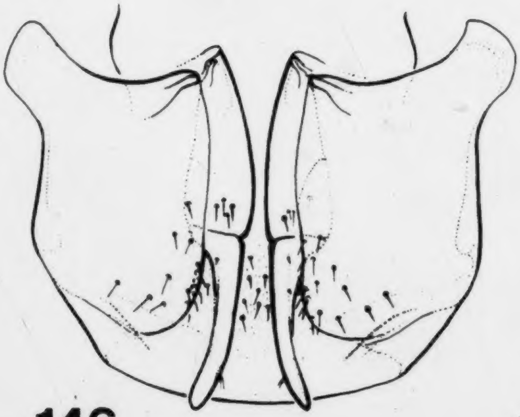
Figure 145. *B. carinula*.

Figure 146. *B. alaskense*.

Figure 147. *B. balli*.


spermatheca
spermathecal duct
spermathecal gland
bursa
S1
sternum IX
sternum X
tergum IX/X
S2

145



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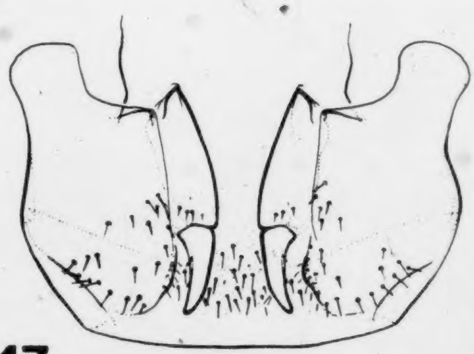


147

Figures 148 to 153. First and second left stylomeres of female genitalia. Scale bar=100µm; all figures at same scale.

Lefthand picture: dorsal view.

Righthand picture: left lateral view.

Figure 148. *B. balli*.

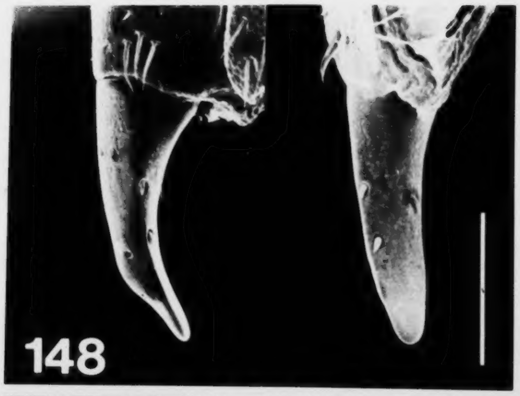
Figure 149. *B. foveum*.

Figure 150. *B. argenteolum*.

Figure 151. *B. alaskense*.

Figure 152. *B. stenoderum*.

Figure 153. *B. punctatostriatum*.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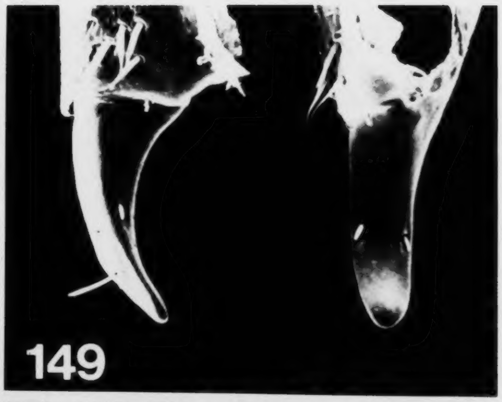
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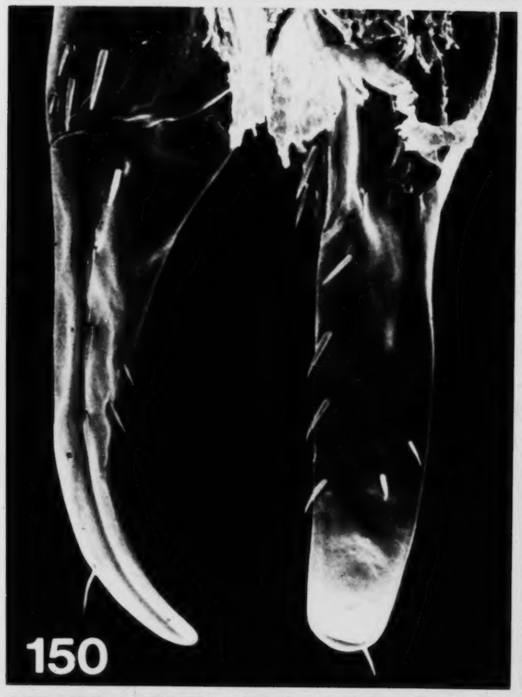
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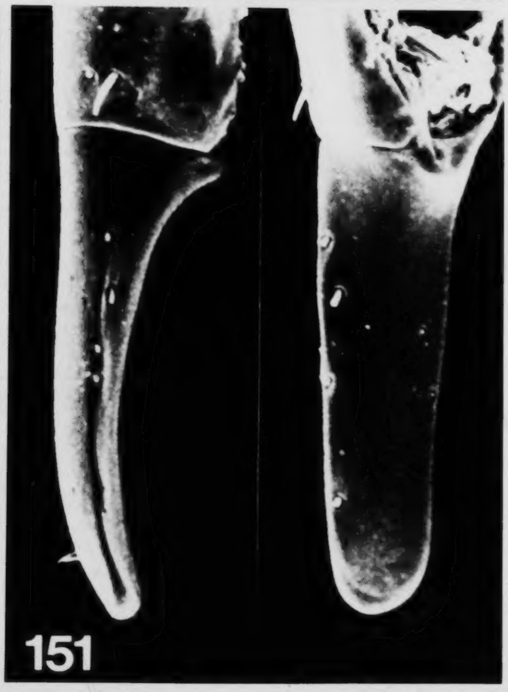
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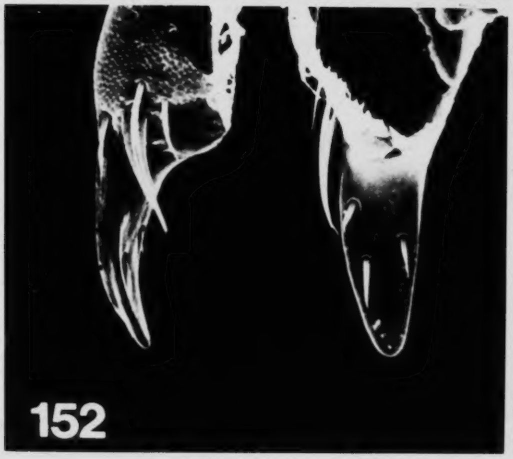
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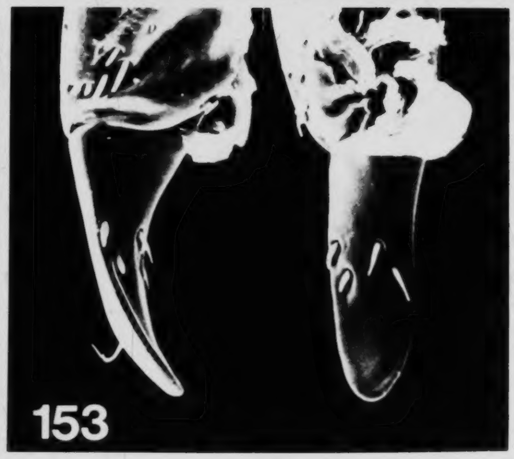

153

Figures 154 to 158. First and second left stylomeres of female genitalia. Scale bar=100μm; all figures at same scale.

Lefthand picture: dorsal view.

Righthand picture: left lateral view.

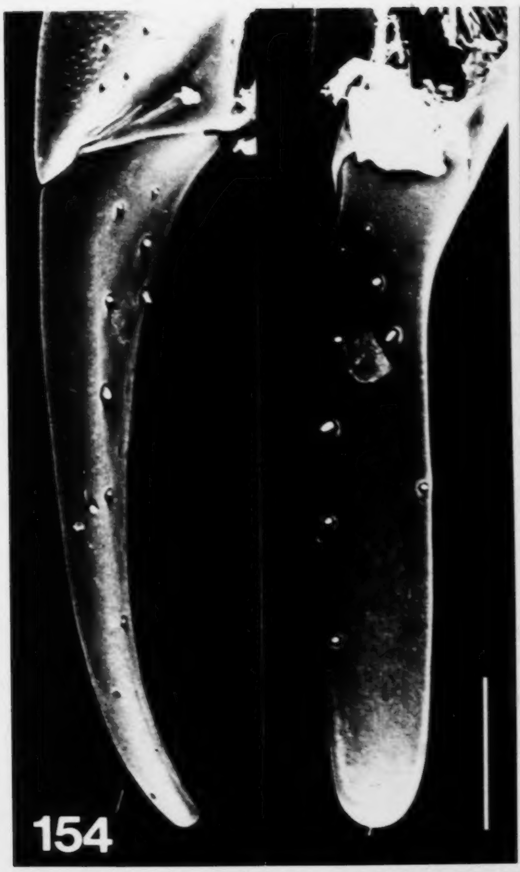
Figure 154. *B. carinula.*

Figure 155. *B. velox.*

Figure 156. *B. lapponicum.*

Figure 157. *B. hesperium.*

Figure 158. *B. lorquinii.*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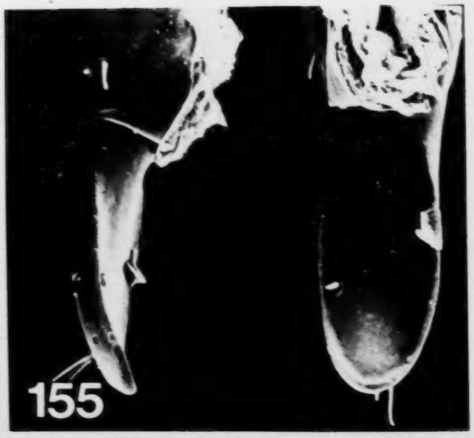
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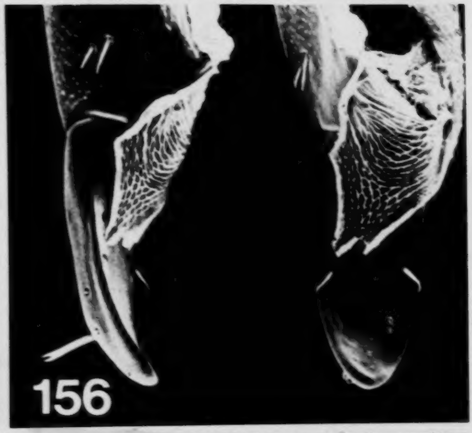
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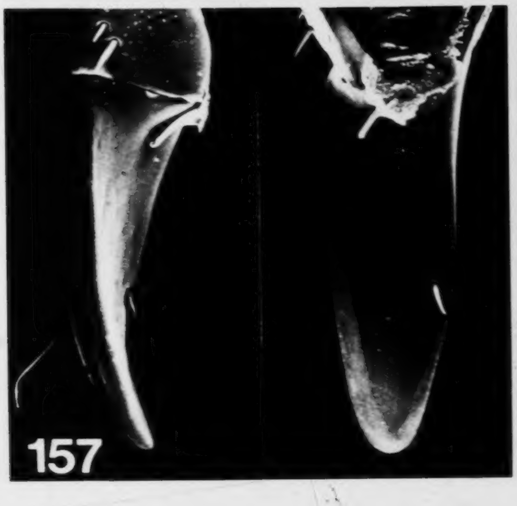
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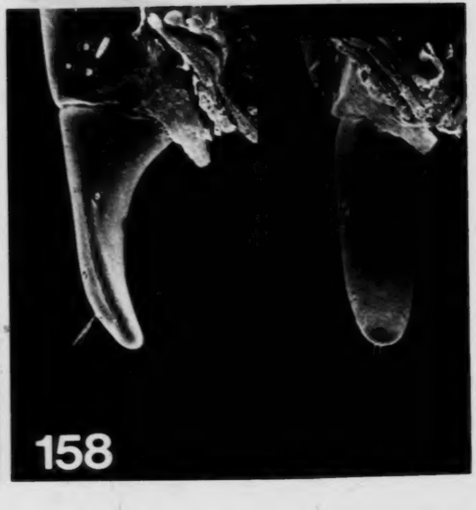

158

Figures 159 to 164. First and second left stylomeres of female genitalia. Scale bar=100µm; all figures at same scale.

Lefthand picture: dorsal view.

Righthand picture: left lateral view.

Figure 159. *B. zephyrum*; specimen from northern Oregon.

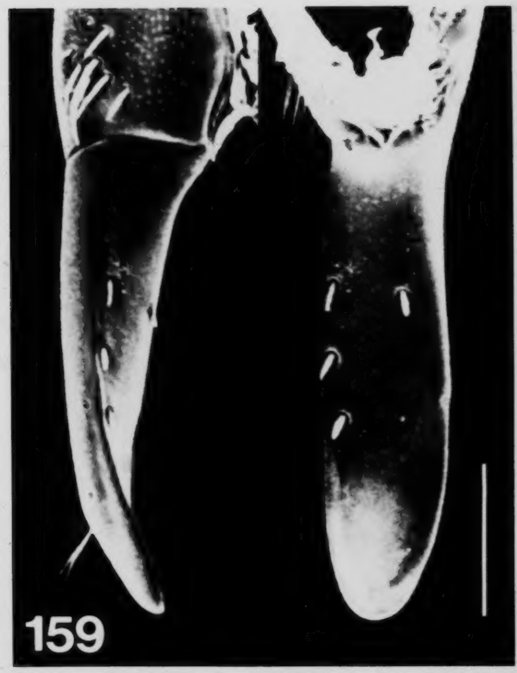
Figure 160. *B. levettei levettei*.

Figure 161. *B. levettei carrianum*.

Figure 162. *B. inaequale*.

Figure 163. *B. litorale*.

Figure 164. *B. baikaloussuricum*.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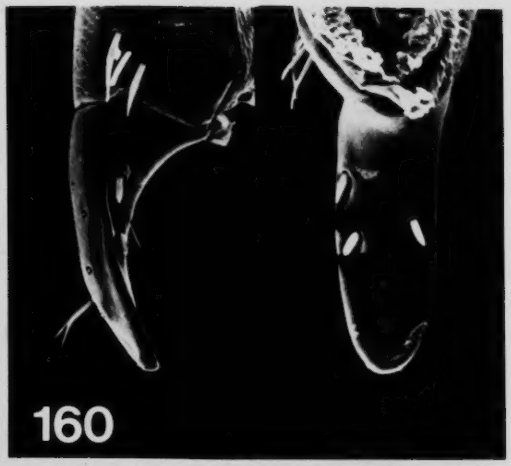
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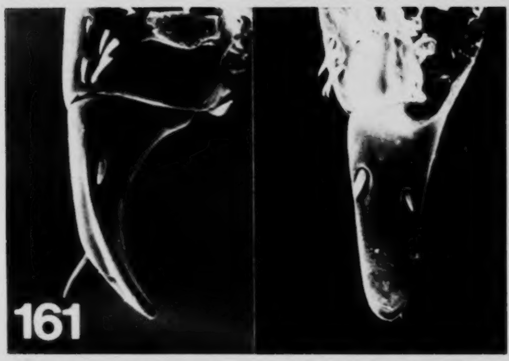
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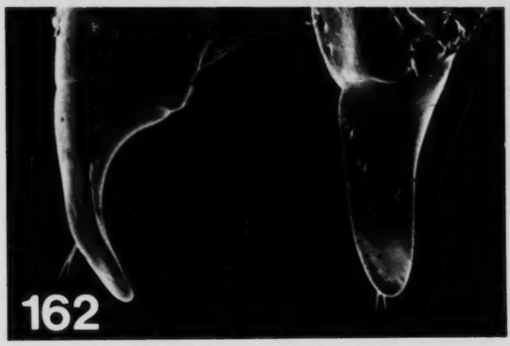
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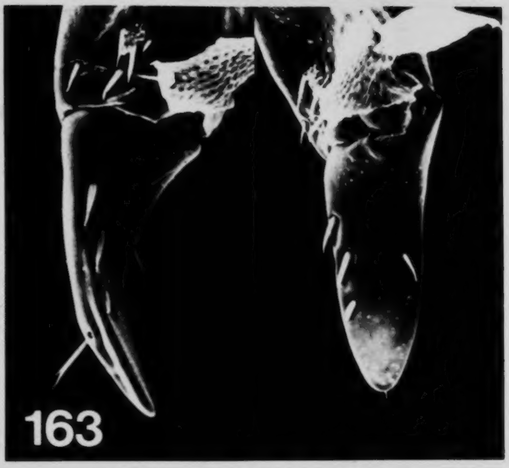
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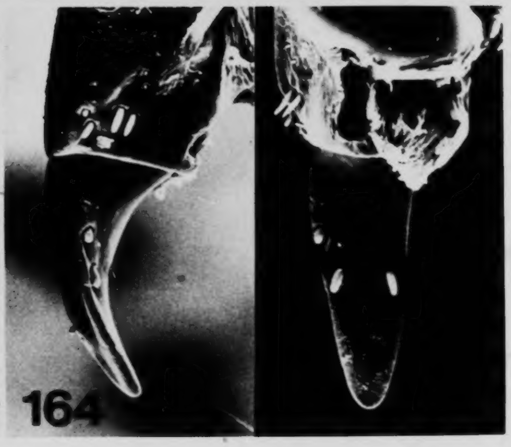

164

Figures 165 to 179. Spermathecae of *Chrysobracteon*. Scale bar=100μm; all figures at same scale.

Figure 165. *B. balli*.

Figure 166. *B. foveum*.

Figure 167. *B. argenteolum*.

Figure 168. *B. alaskense*.

Figure 169. *B. stenoderum*.

Figure 170. *B. carinula*.

Figure 171. *B. velox*.

Figure 172. *B. lapponicum*.

Figure 173. *B. punctatostriatum*.

Figure 174. *B. hesperium*.

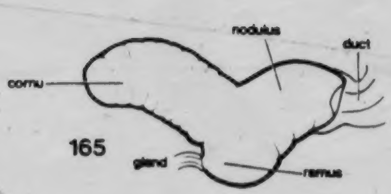
Figure 175. *B. lorquinii*.

Figure 176. *B. zephyrum*.

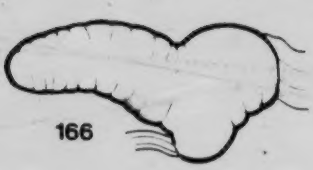
Figure 177. *B. levettei carrianum*.

Figure 178. *B. inaequale*.

Figure 179. *B. litorale*.


nodulus
duct
cornu
gland
ramus

165



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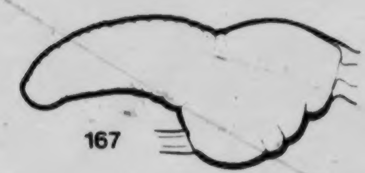

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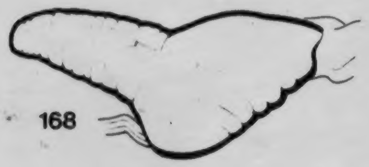

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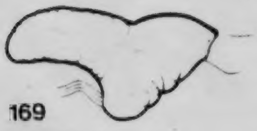

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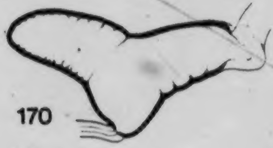

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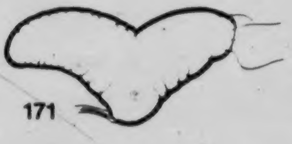

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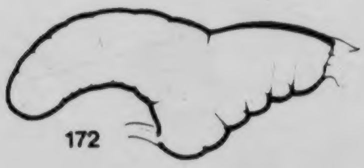

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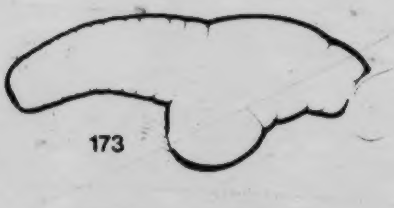

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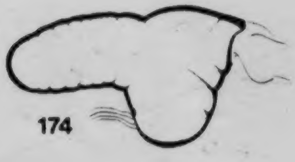

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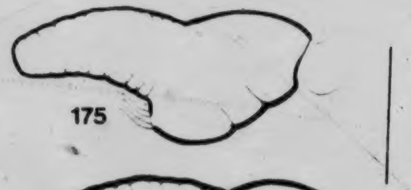

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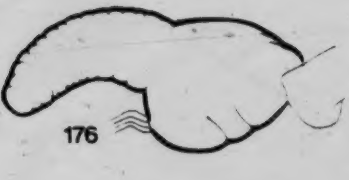

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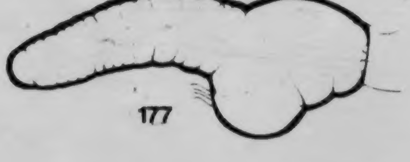

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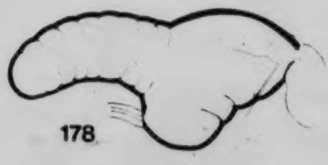

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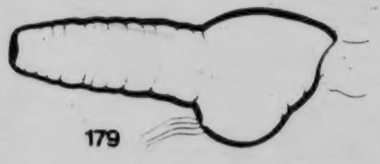


179

Figures 180 to 184.

Figure 180. Left paramere of *B. levettei carrianum.* Right lateral view. Scale bar=100µm.

Figure 181. Right paramere of *B. levettei carrianum.* Left lateral view. Scale as previous figure.

Figure 182. Ring sclerite of *B. levettei carrianum.* Scale bar=.5mm.

Figure 183. Rectal pads of *B. foveum.* Scale bar=.5mm.

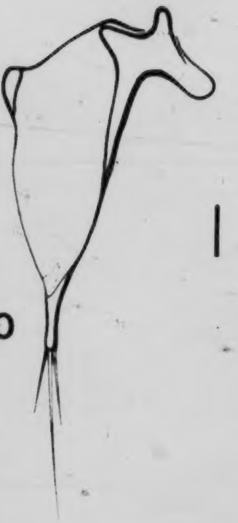
Figure 184. Cleared pygidial defense structures of *B. balli.* Left dorsal view. Scale bar=.5mm.

Figures 185 to 187. Everted female genitalia. Scale bar=.5mm.

Figure 185. Dorso-apical view of everted female genitalia of *B. carinula.*

Figure 186. Dorso-apical view of everted female genitalia of *B. balli.*

Figure 187. Left lateral view of everted female genitalia of *B. carinula.*



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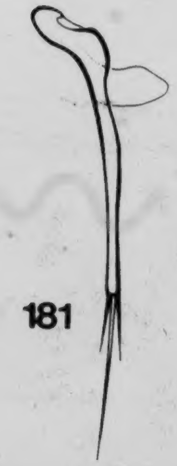

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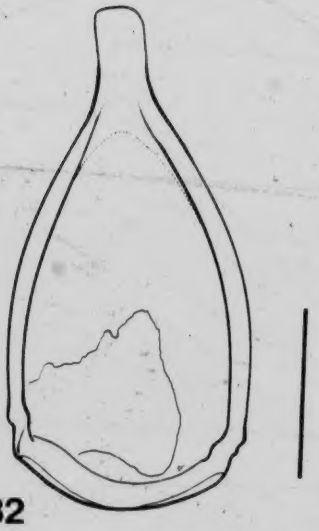

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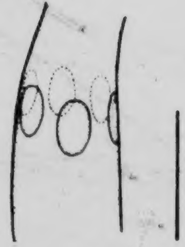

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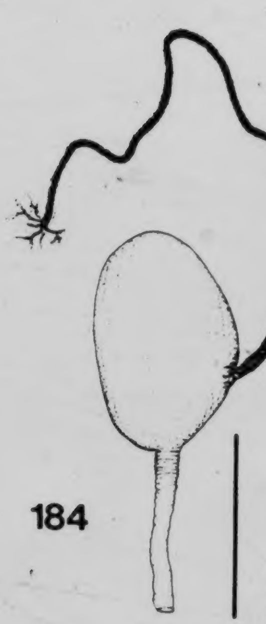

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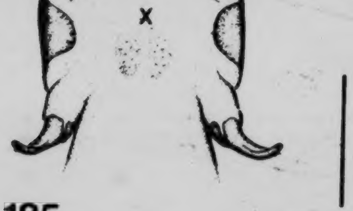

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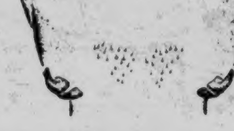

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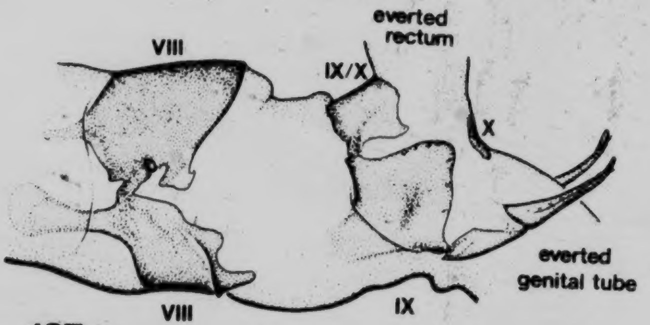

everted
rectum
VIII
IX/X
X
everted
genital tube
VIII
IX

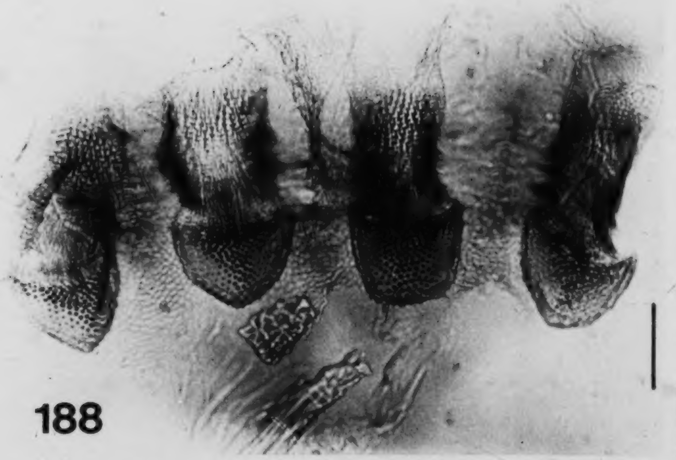
187

Figures 188 to 189. Proventriculi of *Bembidion*. Scale bars=100µm.

Figure 188. *B. carinula*.

Figure 189. *B. (Ocys) harpaloides*. Only one of four lobes shown.

Figure 190. North Saskatchewan River bank at Paynton Ferry, Saskatchewan. Habitat of *B. balli*, *B. foveum*, *B. carinula*, *B. lapponicum*, *B. punctatostriatum*, and *B. levettei carrianum*, as well as the related *B. coxendix* and *B. cheyennense*.



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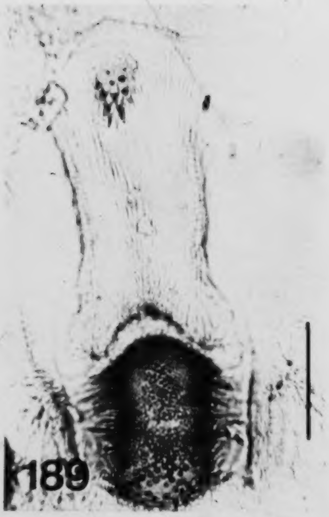
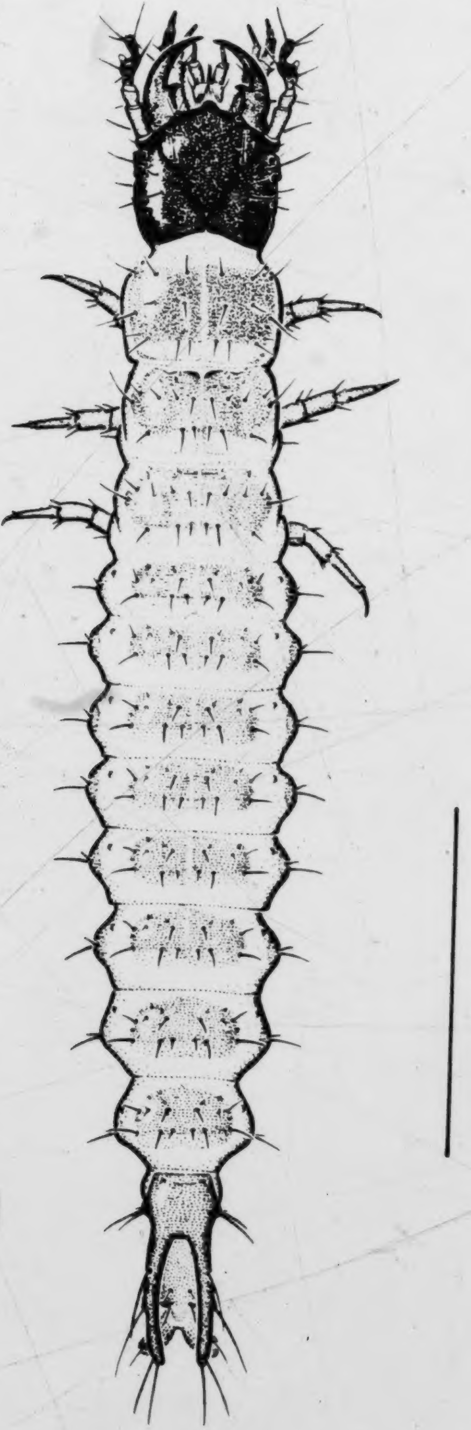


189

190

Figure 191. Dorsal view of first instar *B. balli* larva.
Scale bar=1mm.



191

Figures 192 to 197. Bembidiine larvae. Boxed letters represent the two-letter sclerite or organ code used for sensillar nomenclature. Scale bars all 100µm, except for Fig. 195, for which scale bar=10µm; Figs. 192 and 193 at same scale, as are Figs. 196 and 197.

Figure 192. Nasale of first instar *B. coxendix*.

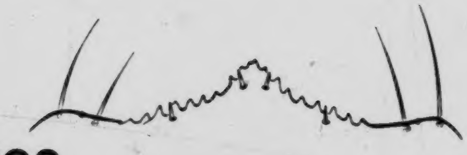
Figure 193. Nasale of first instar *B. inaequale*.

Figure 194. Head of first instar *B. punctatostriatum*, dorsal view.

Figure 195. Apex of seta FR_2 of first instar *Asaphidion alaskanum*.

Figure 196. Right central portion of frontale of first instar *B. balli*.

Figure 197. Right central portion of frontale of first instar *B. carinula*.



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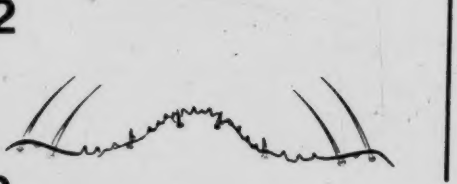

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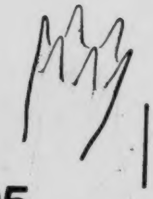

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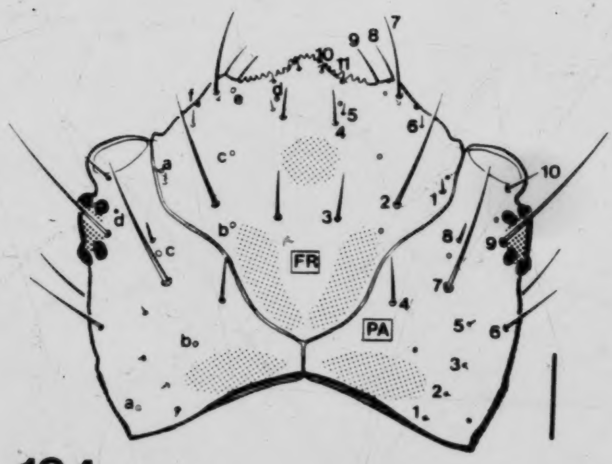
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10 11
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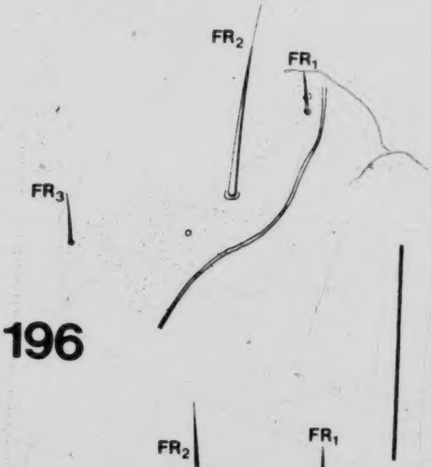
194



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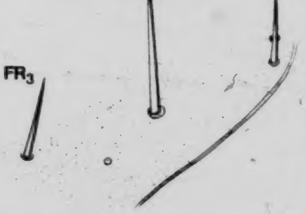


197

Figures 198 to 203. Cleared head structures of larval *Bembidion*. Scale bar=100µm. Boxed letters represent the two-letter sclerite or organ code used for sensillar nomenclature.

Figure 198. Right mandible of first instar *B. carinula*, dorsal view. Note wide mesal shelf.

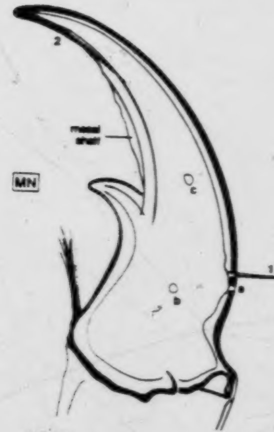
Figure 199. Right mandible of first instar *B. foveum*, dorsal view. Note narrow mesal shelf.

Figure 200. Right mandible of first instar *B. (Odontium) coxendix*, dorsal view.

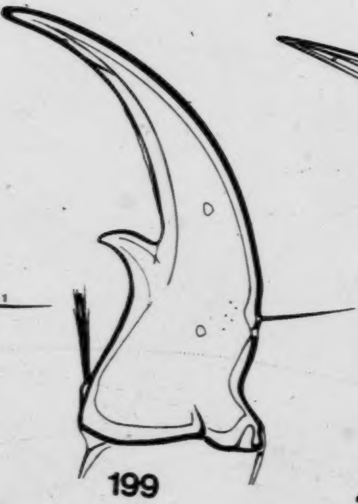
Figure 201. Right antenna of first instar *B. foveum*, dorsal view.

Figure 202. Labium of first instar *B. foveum*, dorsal view.

Figure 203. Right maxilla of first instar *B. foveum*, dorsal view.


MN
2
mesal shelf
c
b
a
1

198



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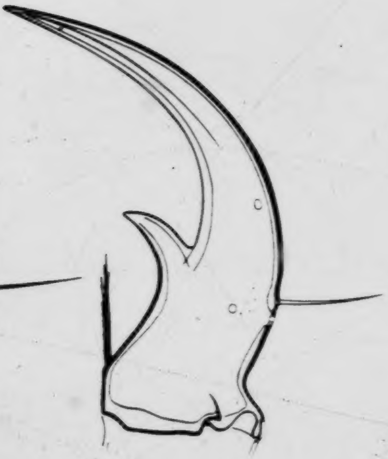

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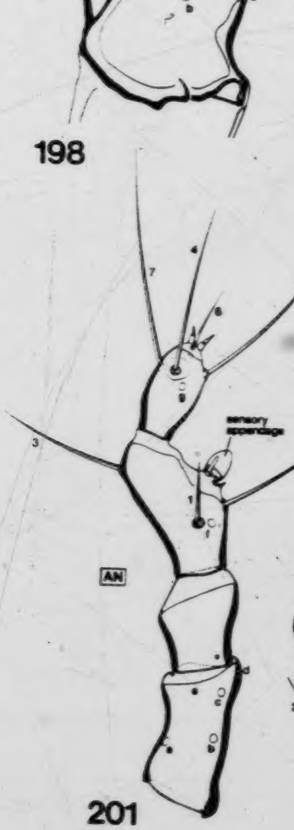
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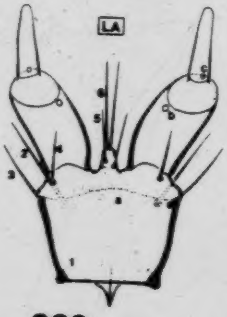
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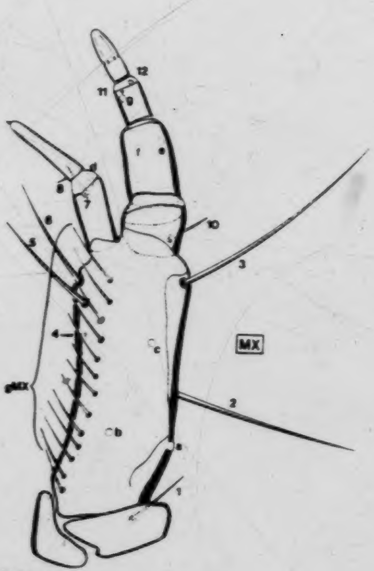
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1

203

Figures 204 to 209. Structures of larval *Chrysobracteon*.

Figure 204. Sensillum FRf in first instar *B. punctatostriatum*. Scale bar=2μm.

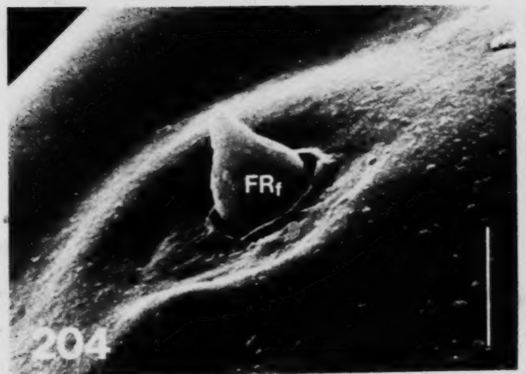
Figure 205. Small sensillum between FR_8 and FR_9 in first instar *B. foveum*. Scale bar=10μm.

Figure 206. Apex of maxillary palpus of first instar *B. lapponicum*. Scale bar=2μm.

Figure 207. Apex of galea of first instar *B. lapponicum*. Scale bar=2μm.

Figure 208. Apical article of labial palpus of first instar *B. lapponicum*. Scale bar=10μm.

Figure 209. Anterior view of ligular region of *B. lapponicum*. Note quadrisetose ligula and multiply branched setae. Scale bar=20μm.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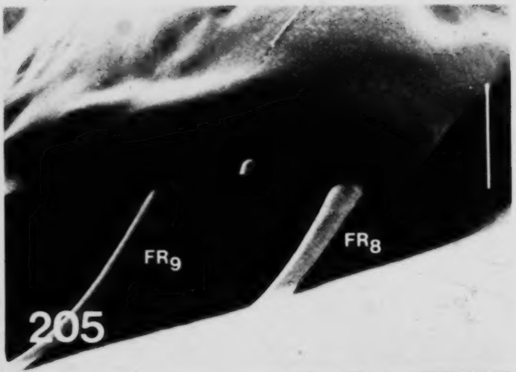
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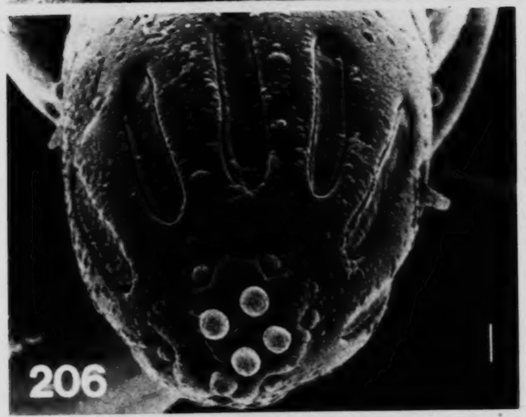
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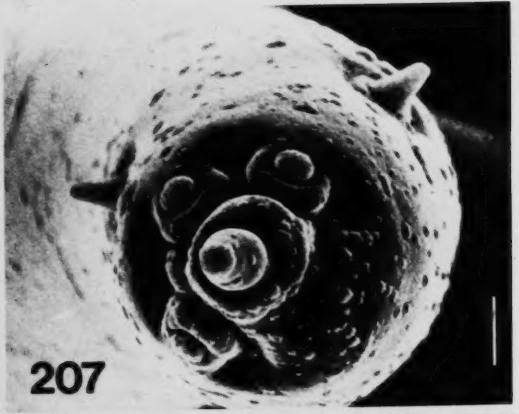
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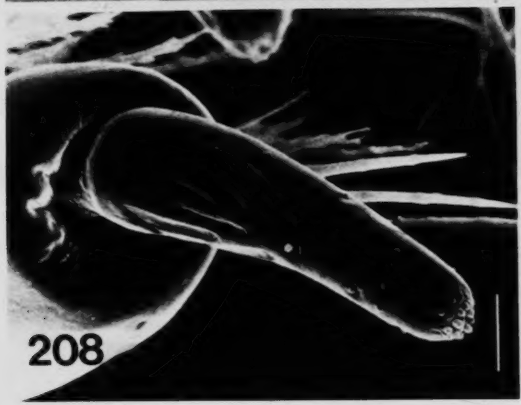
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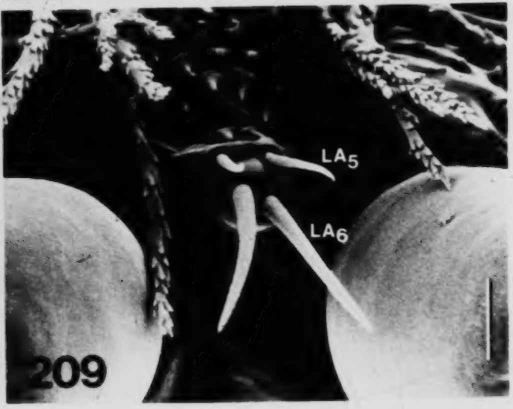
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Figures 210 to 217. Cleared heads of first instar larvae. Scale bar=100μm; all figures at same scale.

Figure 210. *B. balli.*

Figure 211. *B. foveum.*

Figure 212. *B. alaskense.*

Figure 213. *B. carinula.*

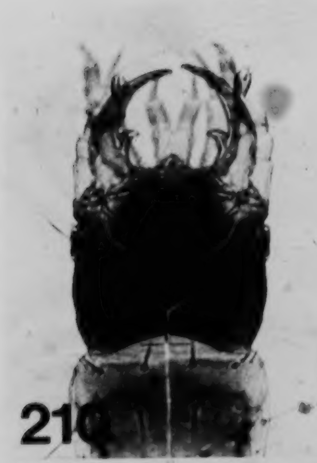
Figure 214. *B. lapponicum.*

Figure 215. *B. punctatostriatum.*

Figure 216. *B. lorquinii.*

Figure 217. *B. zephyrum.*

Figure 218. Cleared head of second instar *B. levettei levettei* larva. Same scale as Figs. 210-217.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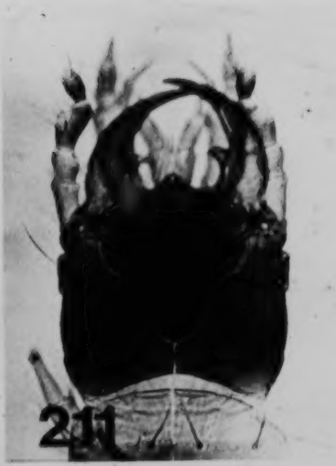
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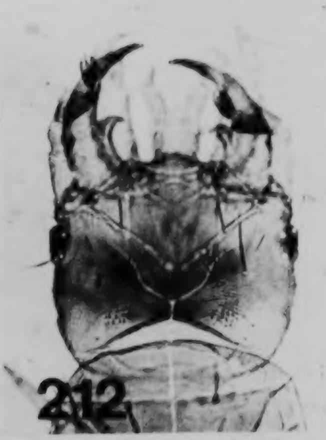
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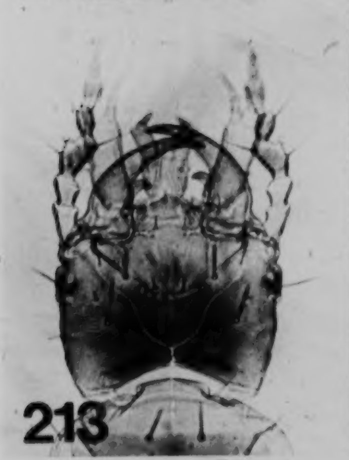
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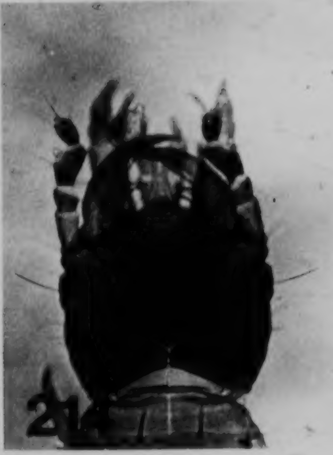
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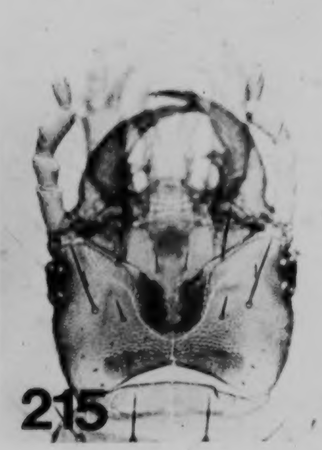
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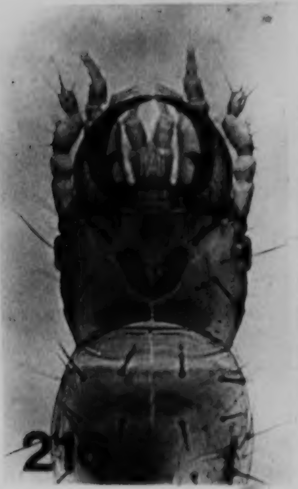
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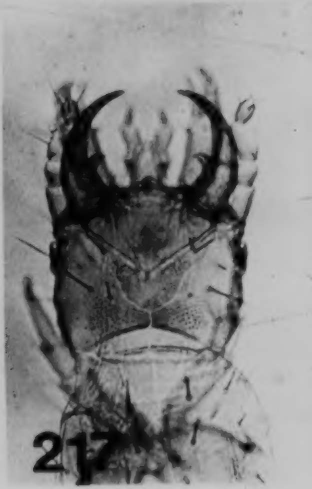
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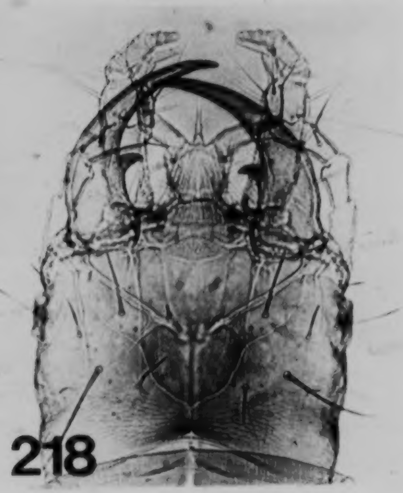
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Figures 219 to 225. Cleared heads of first instar larvae. Scale bar=100µm; all figures at same scale.

Figure 219. *B. coxendix.*

Figure 220. *B. cheyennense.*

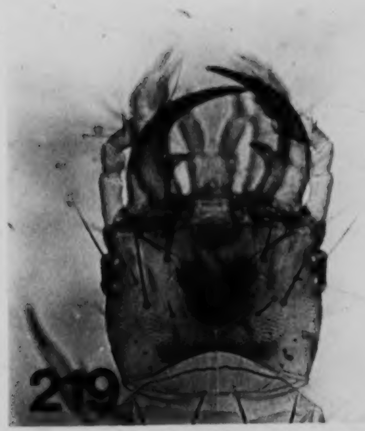
Figure 221. *B. chalceum.*

Figure 222. *B. antiquum.*

Figure 223. *B. aenulum.*

Figure 224. *B. obtusum.*

Figure 225. *Asaphidion alaskanum.*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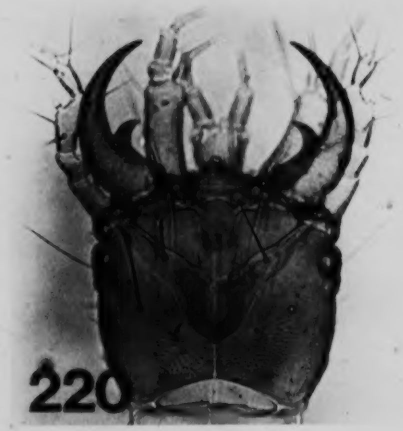
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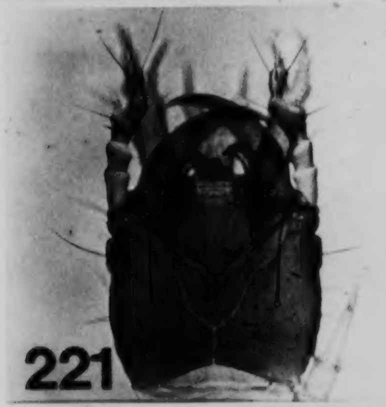
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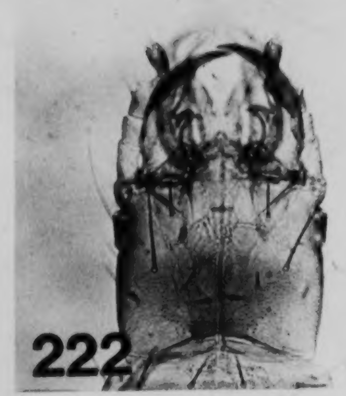
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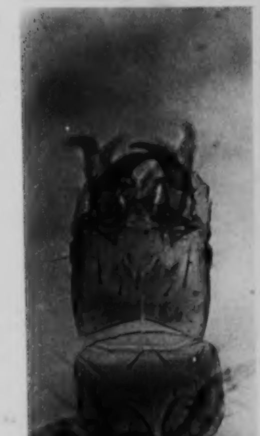
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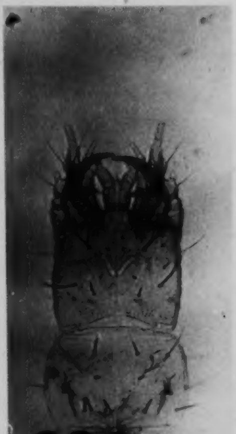
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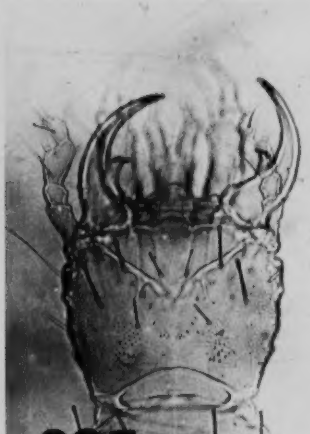
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Figures 226 to 231. First instar *Chrysobracteon*, central and right portions of posterior part of head. Scale bar=40μm.

Figure 226. *B. foveum.*

Figure 227. *B. alaskense.*

Figure 228. *B. carinula.*

Figure 229. *B. lapponicum.*

Figure 230. *B. punctatostriatum.*

Figure 231. *B. levettei levettei.*

Figures 232 to 235. Parietal egg bursters. Scale bar=40μm.

Figure 232. *B. foveum.*

Figure 233. *B. alaskense.*

Figure 234. *B. carinula.*

Figure 235. *B. lapponicum.*

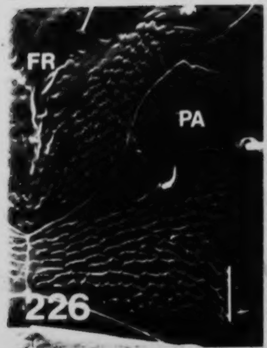
Figures 236 to 239. First instar *Chrysobracteon*.

Figure 236. Right basal corner of pronotum of *B. alaskense*. Scale bar=40μm.

Figure 237. Right basal corner of pronotum of *B. punctatostriatum*. Scale bar=40μm.

Figure 238. Dorsal view of nasale and mouth cavity of *B. foveum*. Scale bar=40μm.

Figure 239. Dorsal view of right mandible of *B. punctatostriatum* near seta MN_1. Scale bar=40μm.



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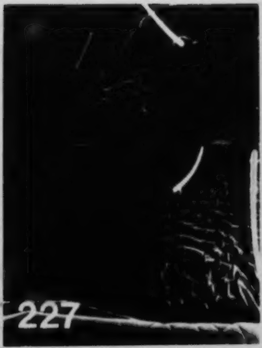

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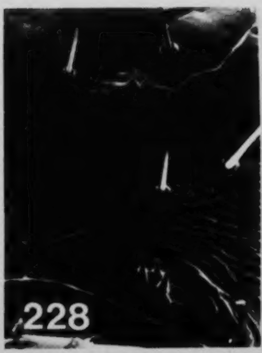

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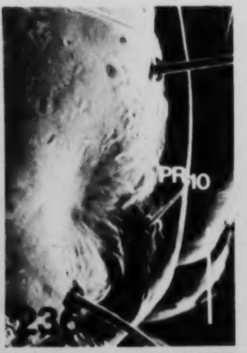

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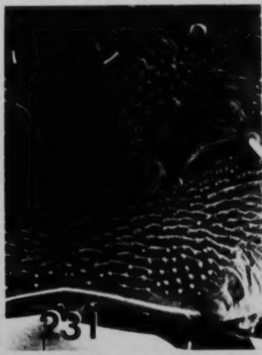

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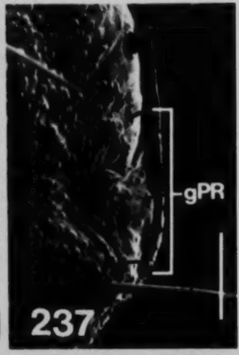

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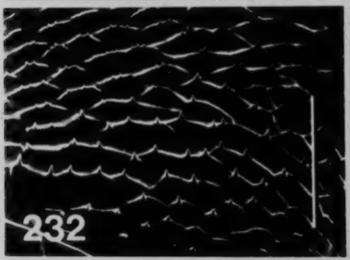

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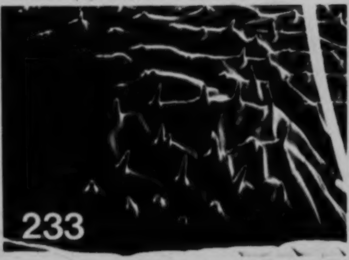

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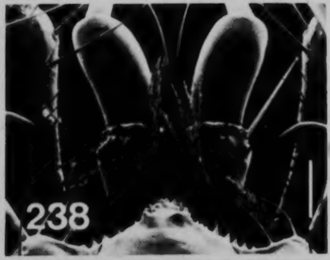

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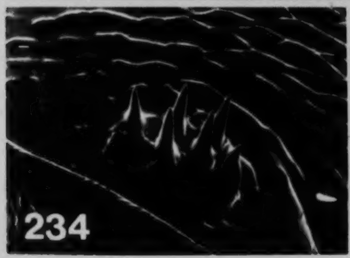

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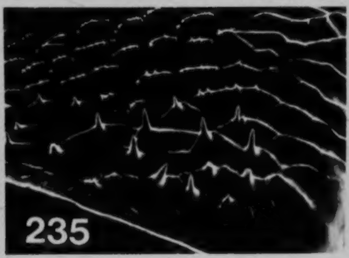

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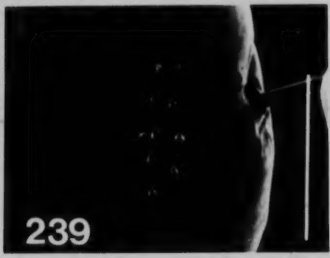

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Figures 240 to 247. Thoraces of larval *Bembidion*. Boxed letters represent the two-letter sclerite or organ code used for sensillar nomenclature. Figs. 240-241 at same scale, scale bar=200µm. Figs. 242-247 at same scale, scale bar=100µm.

Figure 240. Pronotum and mesonotum of first instar *B. balli*.

Figure 241. Pronotum of first instar *B. punctatostriatum*.

Figure 242. Right basilateral corner of pronotum of first instar *B. balli*.

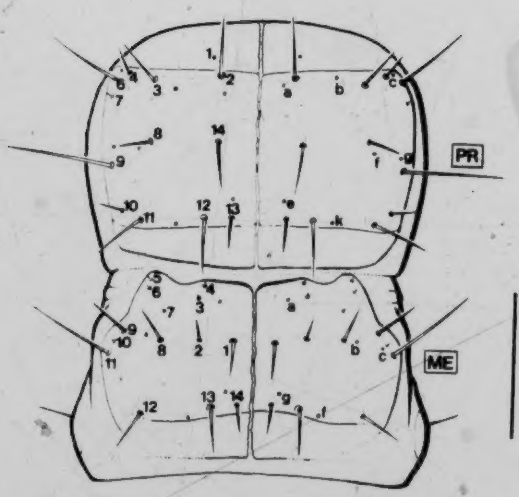
Figure 243. Right basilateral corner of pronotum of first instar *B. carinula*.

Figure 244. Right basilateral corner of pronotum of first instar *B. integrum*.

Figure 245. Right-central portion of mesonotum of first instar *B. balli*.

Figure 246. Right-central portion of mesonotum of first instar *B. carinula*.

Figure 247. Right-central portion of mesonotum of first instar *B. antiquum*.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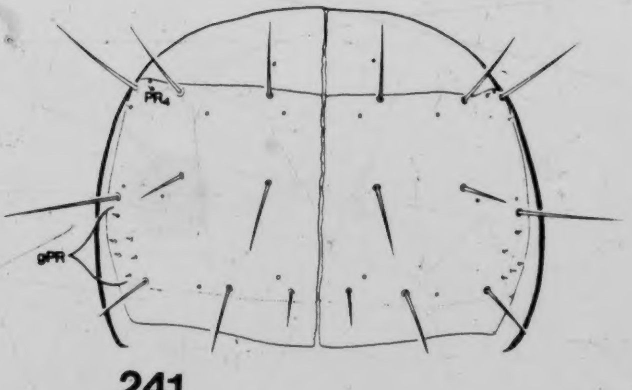

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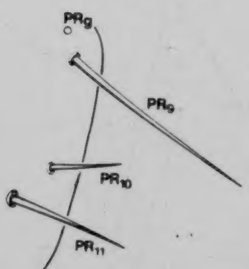
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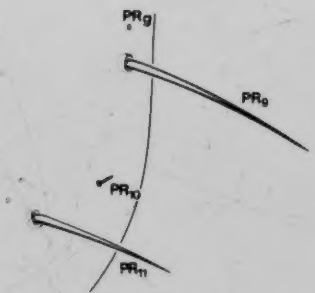
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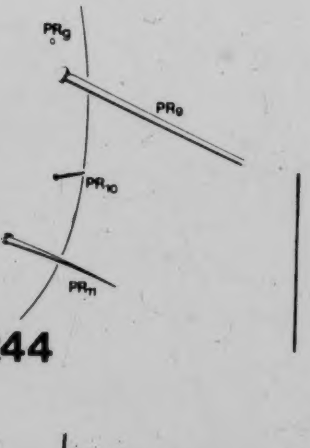
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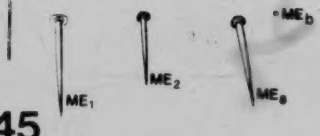
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ME2
MEb
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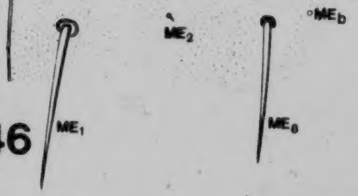
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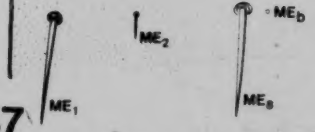

ME1
ME2
MEb
ME8

247

Figures 248 to 251. Second abdominal terga of first instar *Chrysobracteon*. Boxed letters represent the two-letter sclerite or organ code used for sensillar nomenclature. All at same scale; scale bar=100µm.

Figure 248. *B. balli.*

Figure 249. *B. foveum.*

Figure 250. *B. carinula.*

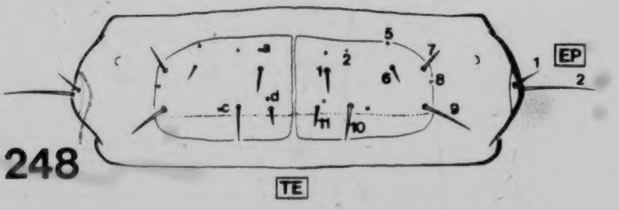
Figure 251. *B. punctatostriatum.*

Figures 252 to 254. Right anterior portion of second abdominal terga of first instar *Chrysobracteon*, showing variation in sizes of seta TE_6. All at same scale; scale bar=100µm.

Figure 252. *B. balli.*

Figure 253. *B. carinula.*

Figure 254. *B. punctatostriatum.*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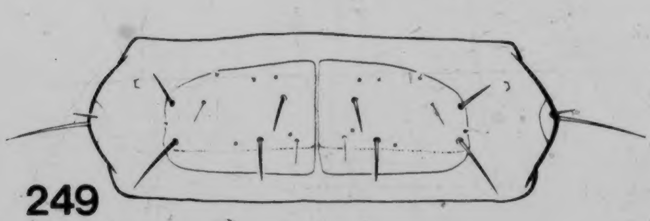

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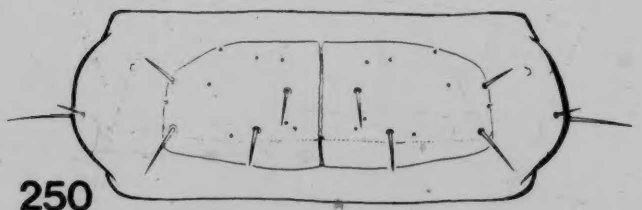

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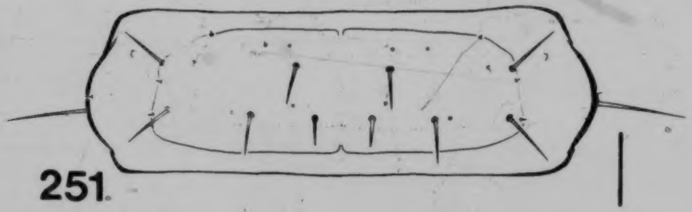

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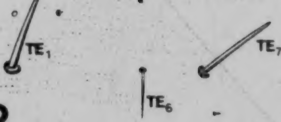

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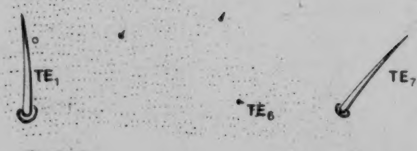

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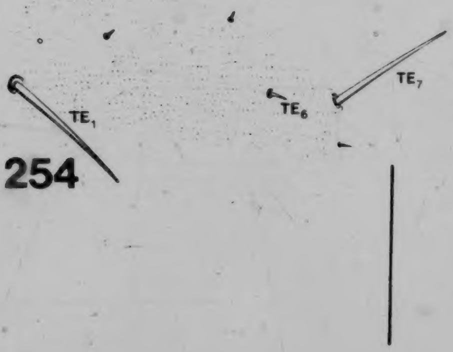


254

Figure 255. Ventral view of abdominal segments VIII through X of first instar *B. balli*. Scale bar=200μm.

Figure 256. Ventral view of abdominal segment IX of first instar *B. carinula*. Same scale as Fig. 255.

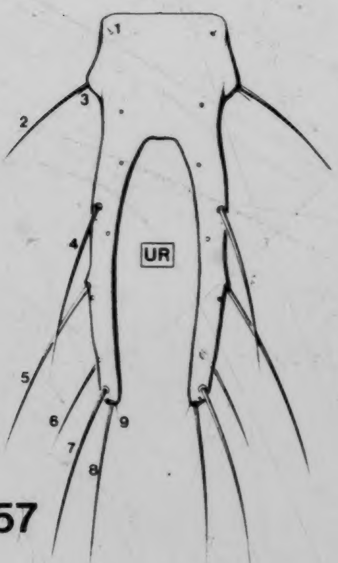
Figures 257 to 260. Urogomphi of *Chrysobracteon*, dorsal view.

Figure 257. First instar *B. balli*. Same scale as Fig. 255.

Figure 258. Second instar *B. balli*. Scale bar=200μm.

Figure 259. Second instar *B. lapponicum*. Same scale as Fig. 258.

Figure 260. Second instar *B. carinula*. Same scale as Fig. 258.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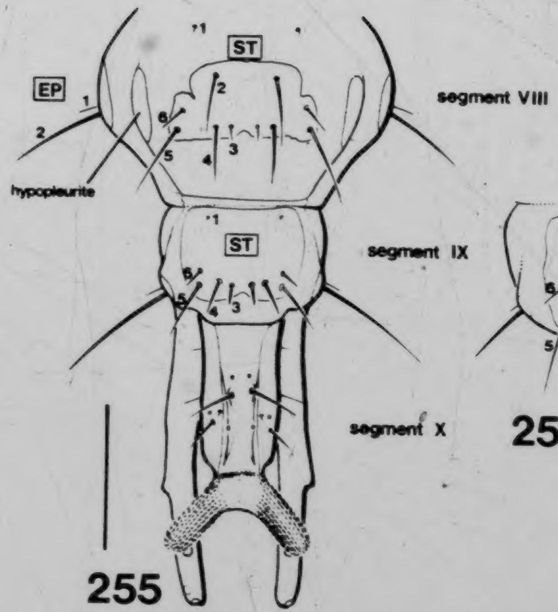
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hypopleurite
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segment IX
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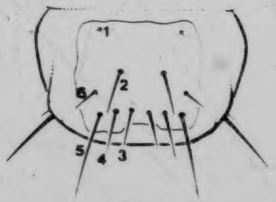
segment X

255



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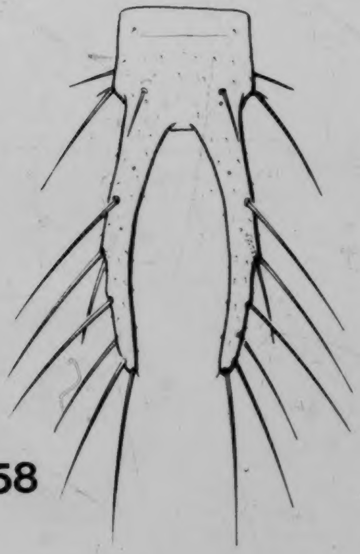
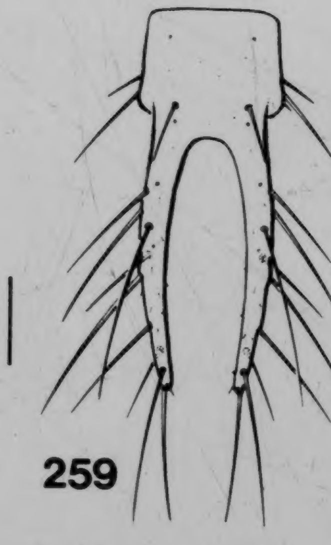


258



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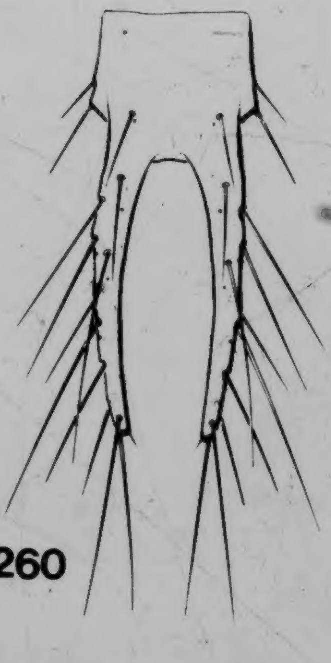

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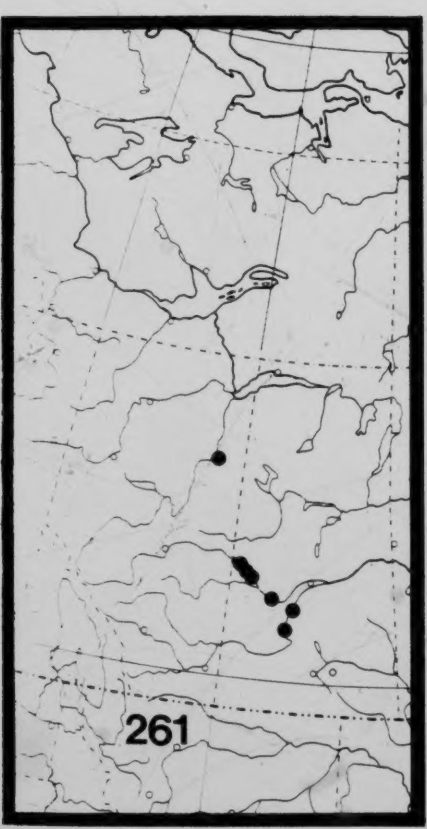
Figures 261 to 262. Geographic distributions of species of *Chrysobracteon*.

Figure 261. *B. balli*.

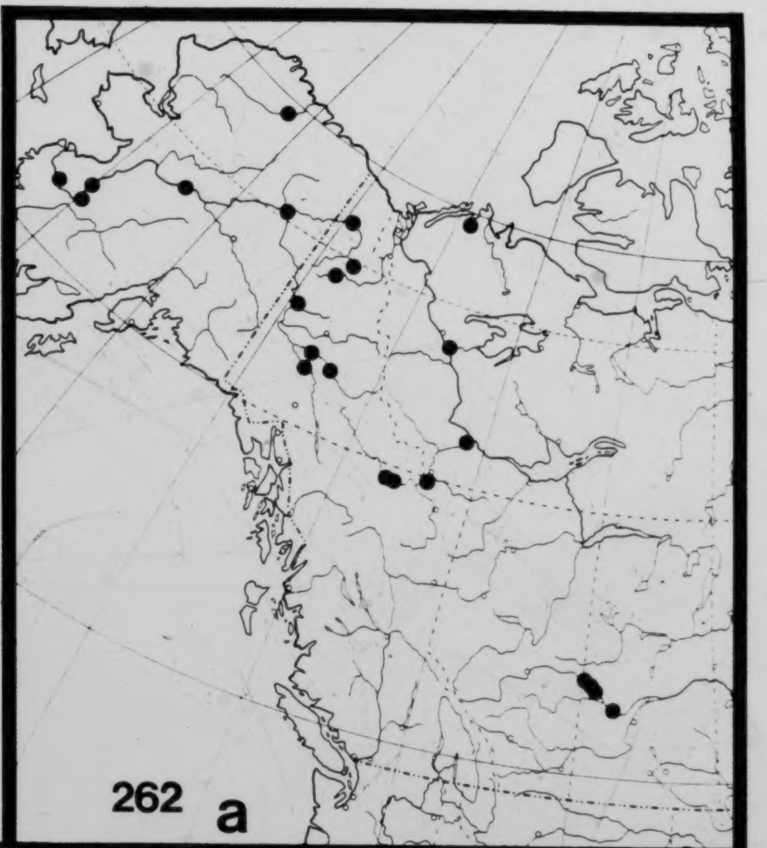
Figure 262. *B. foveum*.

a. Nearctic distribution.

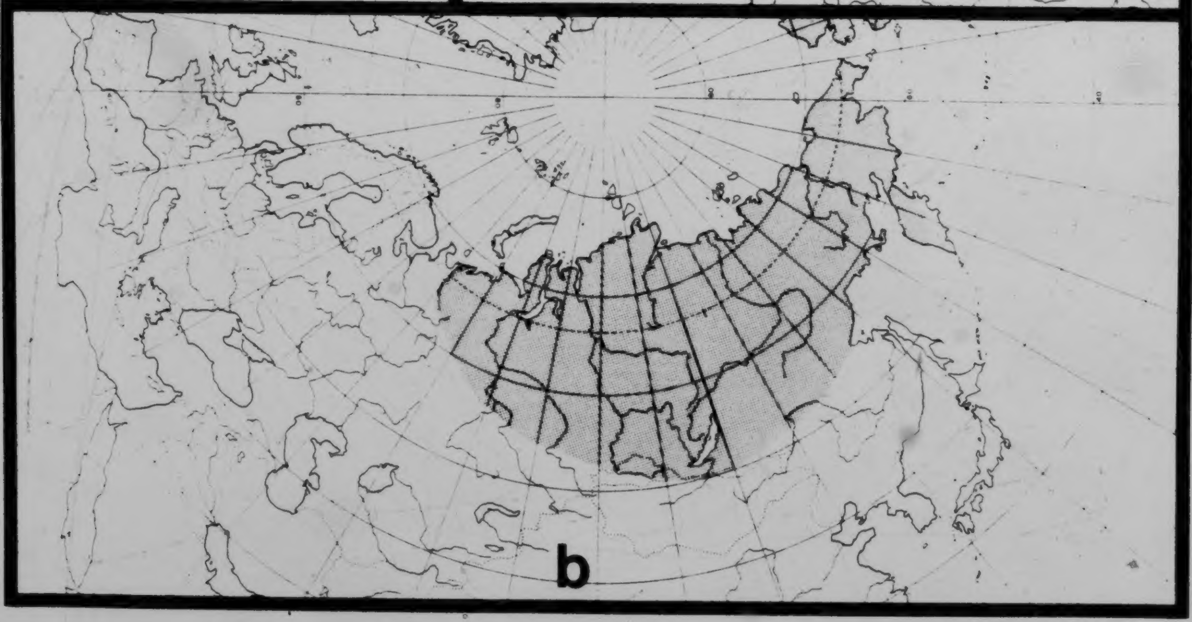
b. Approximate Palearctic distribution. Based on Lindroth (1962) and personal observations.



261



262 a

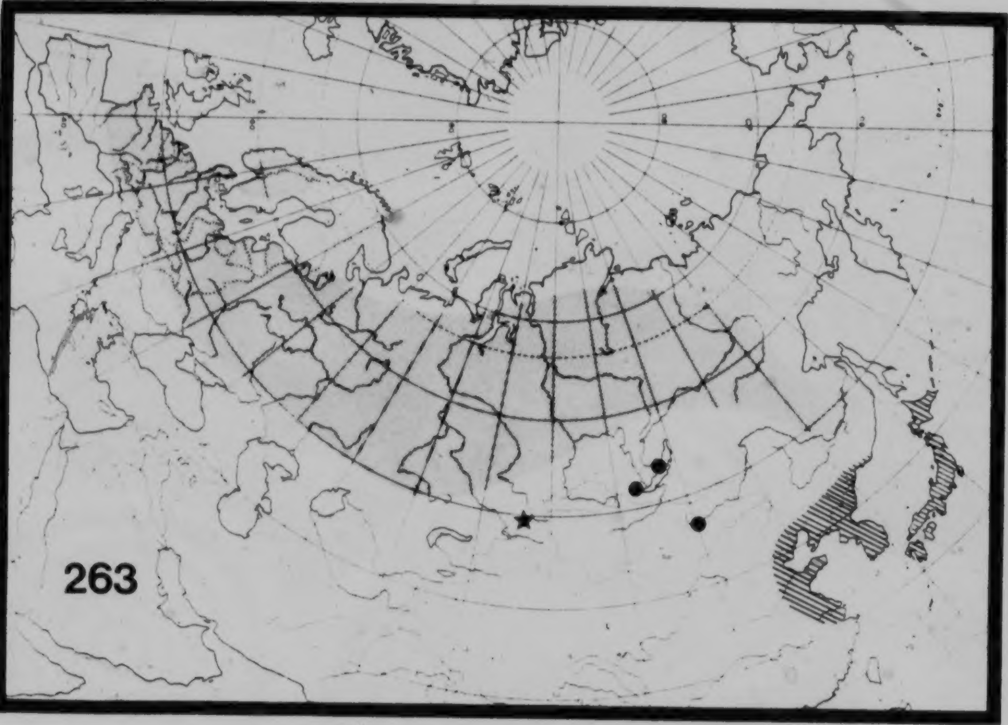


b

Figures 263 to 264. Geographic distributions of species of *Chrysobracteon*.

Figure 263. *B. argenteolum* (stippled), Palearctic *B. alaskense* (dots), *B. semenovi* (star), and *B. stenoderum* (striped). Approximate distributions of *B. argenteolum* and *B. stenoderum* based on Lindroth (1962), Netolitzky and Meyer (1933), Turin *et al.* (1977), and personal observations.

Figure 264. Nearctic distribution of *B. alaskense*.



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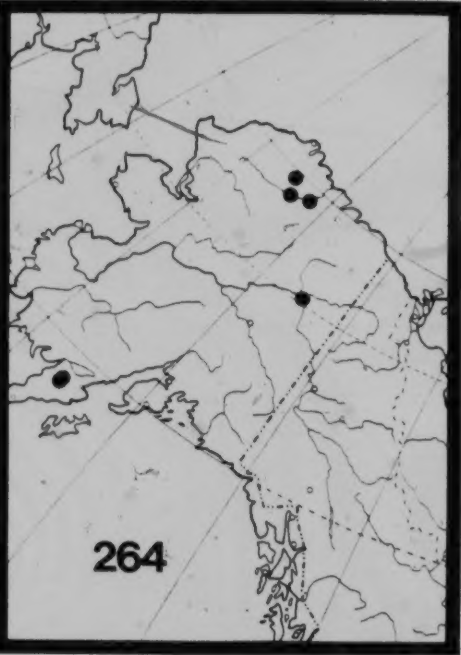

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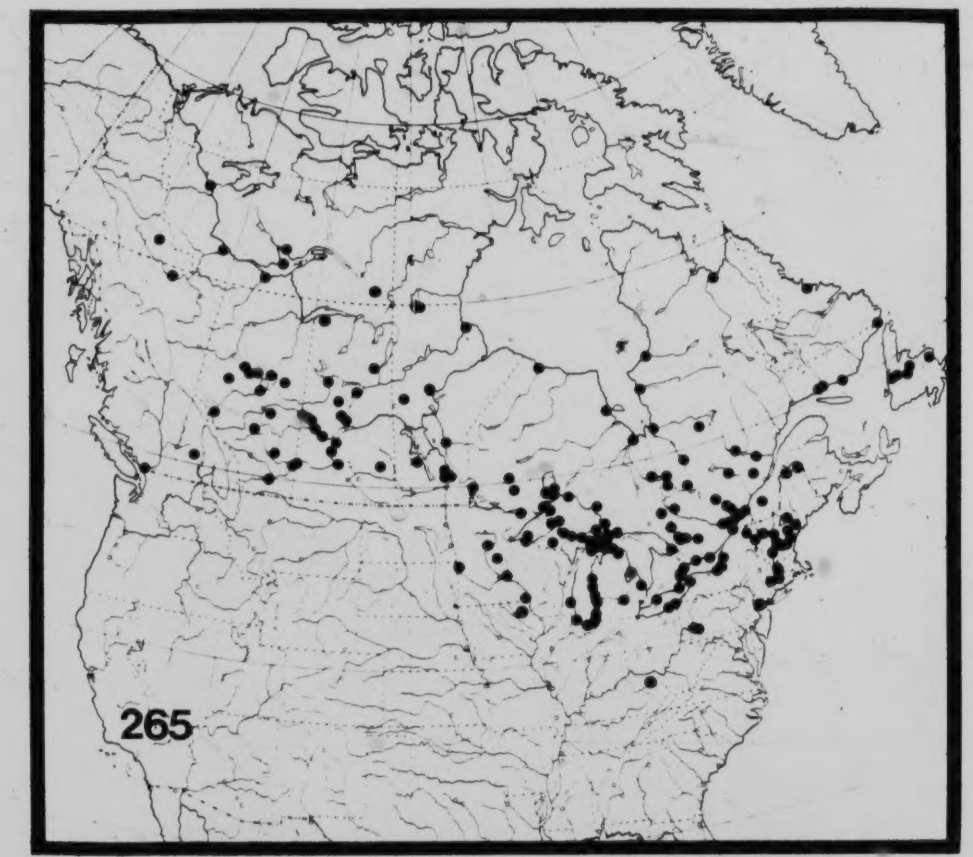
Figures 265 to 266. Geographic distributions of species of *Chrysobracteon*.

Figure 265. *B. carinula*; circled stars represent state records.

Figure 266. *B. velox*. Based on Lindroth (1962), Netolitzky and Meyer (1939), Turin *et al.* (1977), and personal observations.



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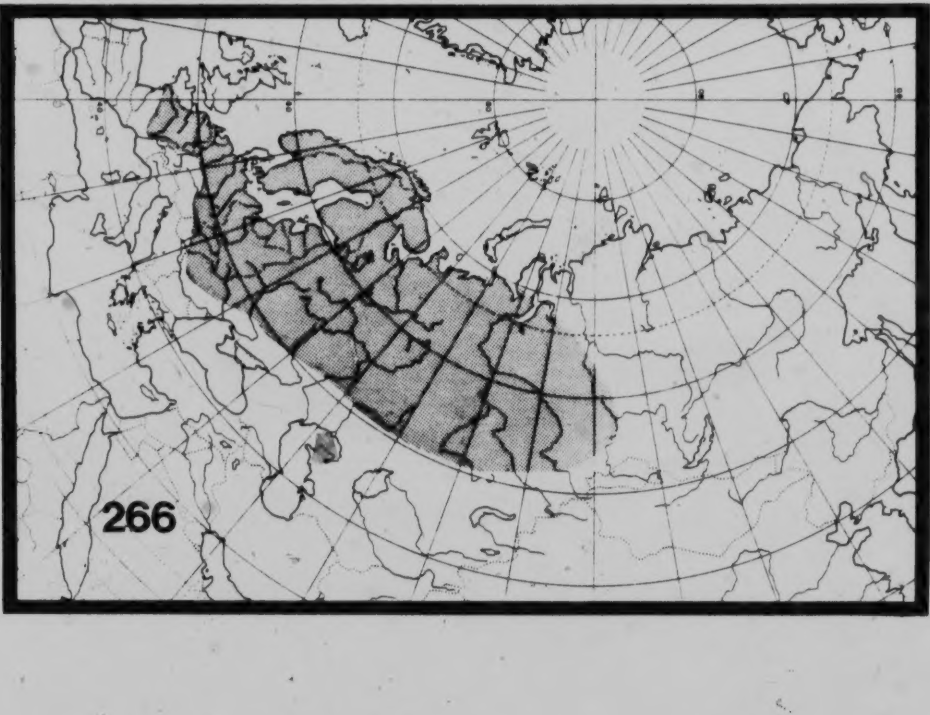

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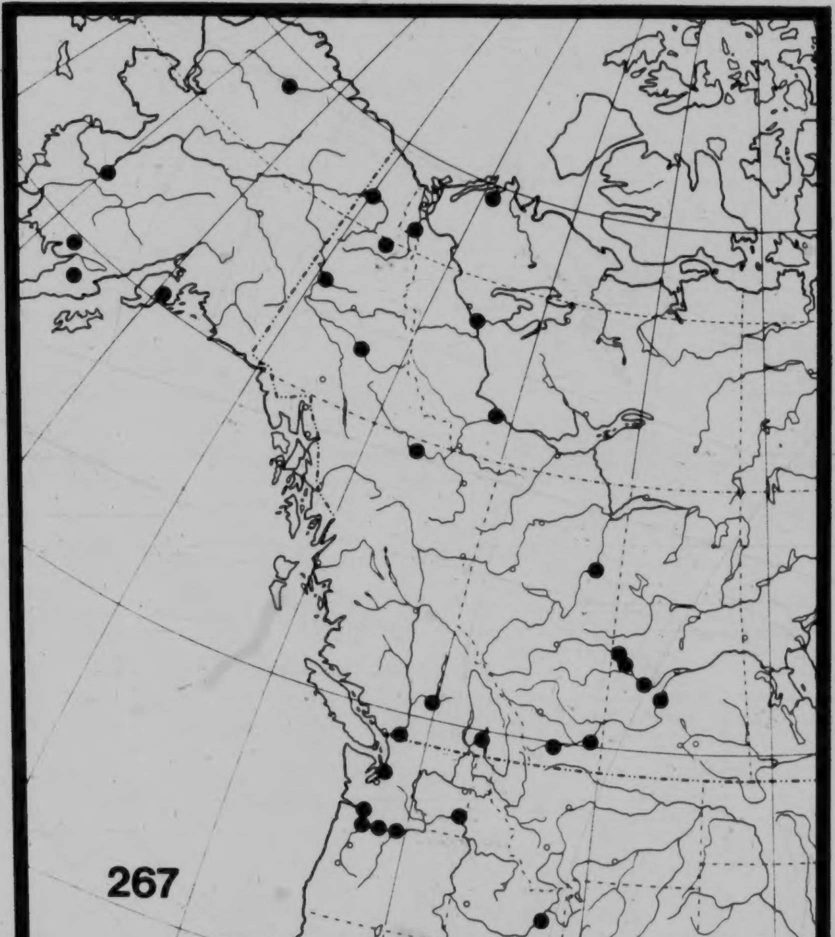
Figure 267. Geographic distribution of *B. lapponicum*.

a. Nearctic distribution.

b. Approximate Palearctic distribution. Based on Lindroth (1962) and personal observations.


267
a
b

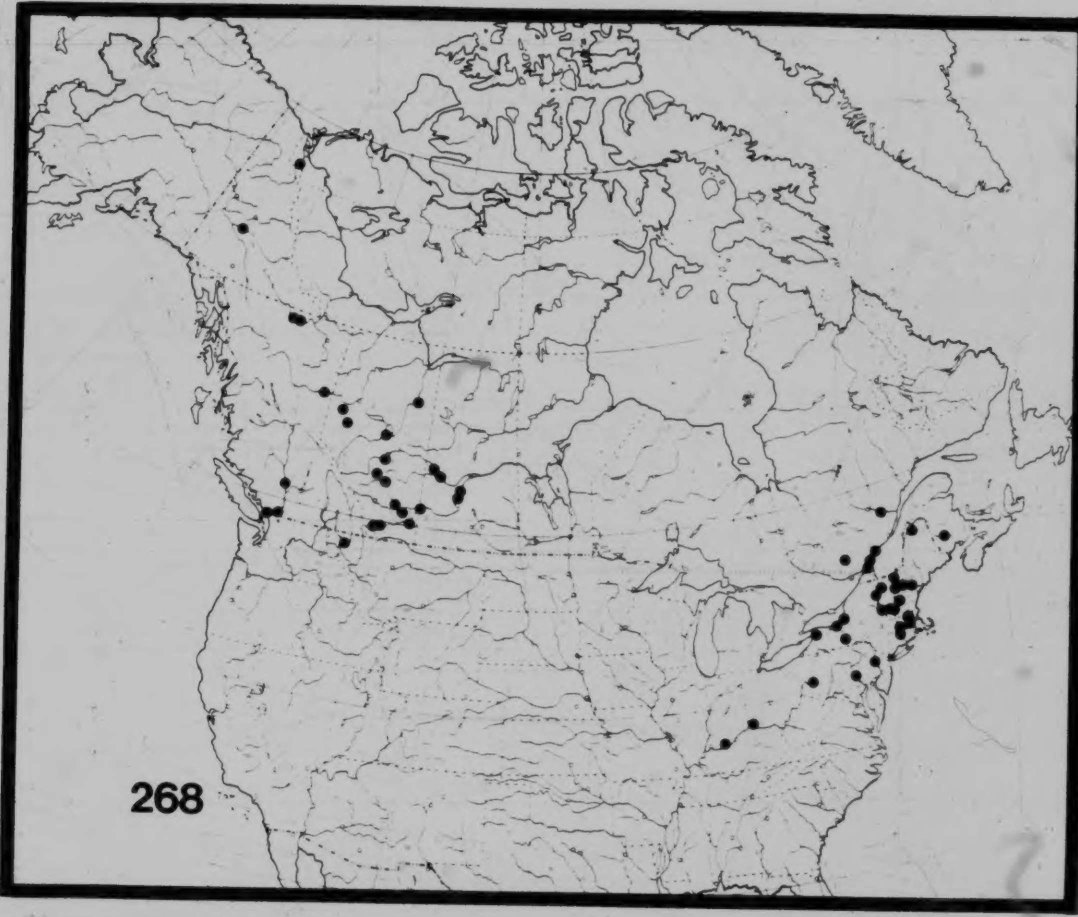
Figures 268 to 271. Geographic distributions of species of *Chrysobracteon*.

Figure 268. *B. punctatostriatum.*

Figure 269. *B. hesperium.*

Figure 270. *B. lorquinii.*

Figure 271. *B. zephyrum.*



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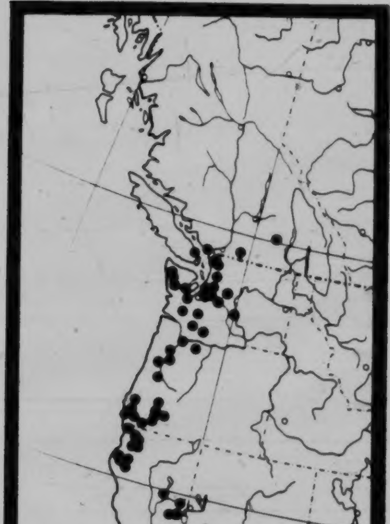

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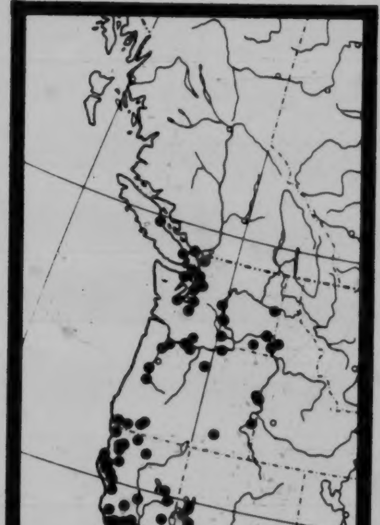

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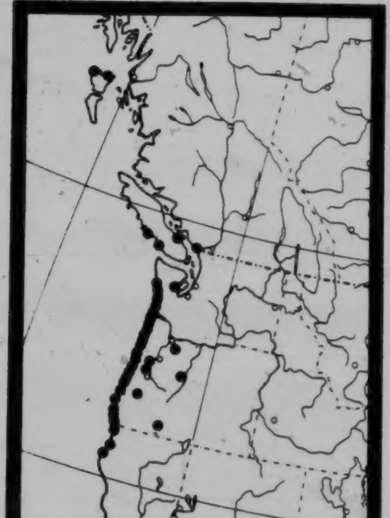

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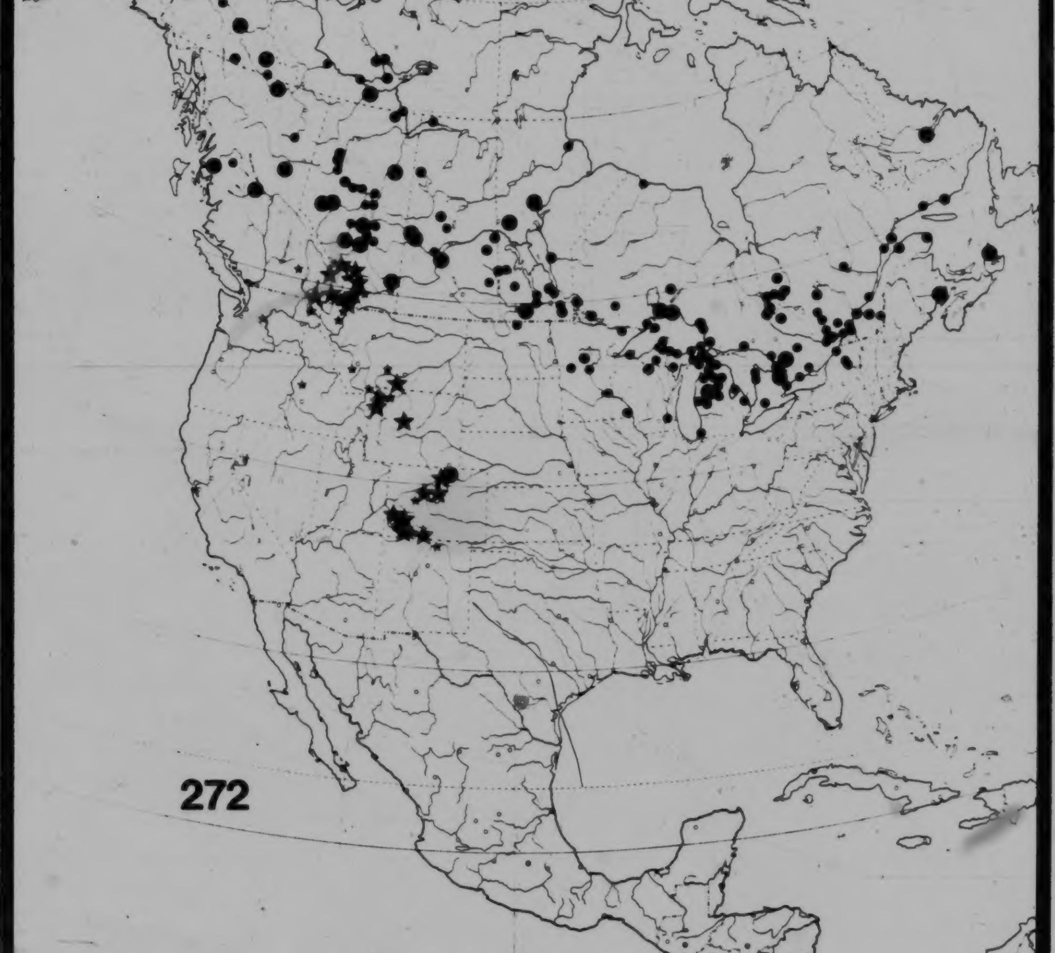
Figure 272. Geographic distribution of *B. levettei*. *B. levettei levettei* (stars) and *B. levettei carrianum* (dots). Localities of specimens identified using male genitalia indicated by larger symbols.



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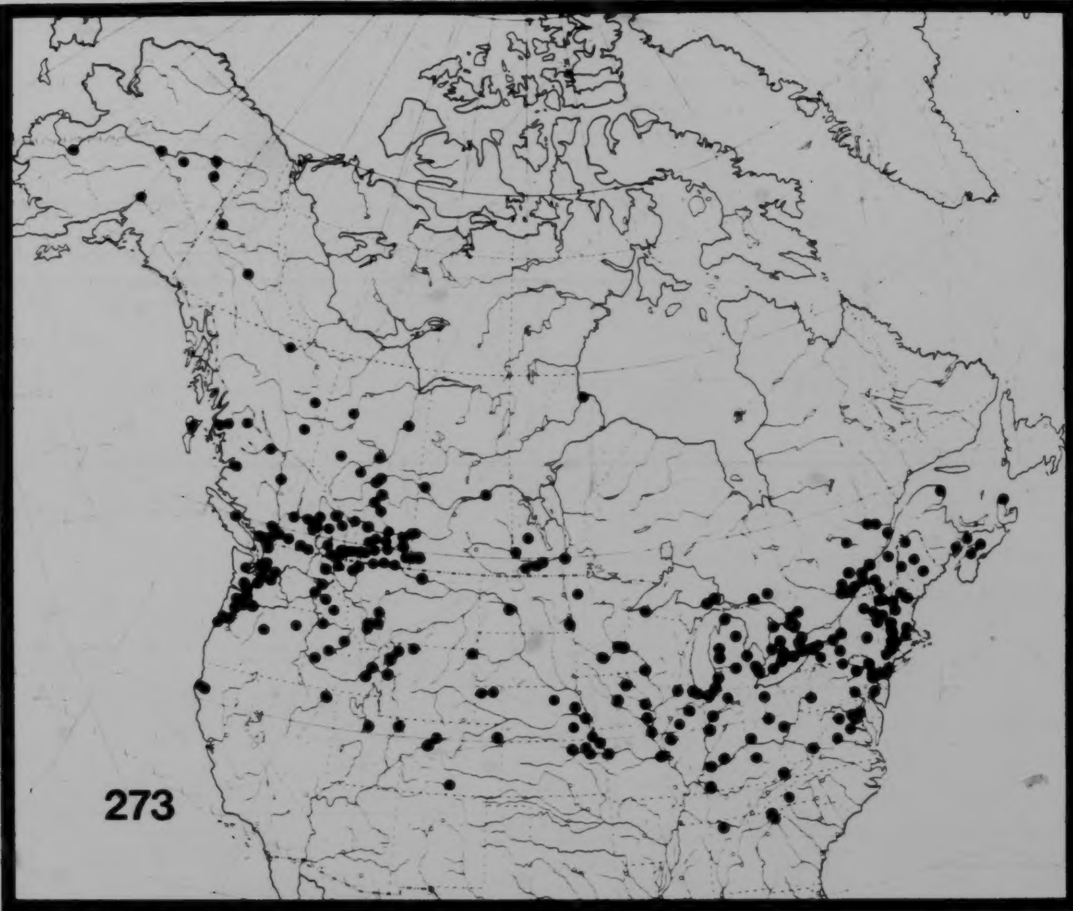
Figures 273 to 274. Geographic distributions of species of *Chrysobracteon*.

Figure 273. *B. inaequale*.

Figure 274. Approximate distributions of *B. litorale* (stippled) and *B. baikaloussuricum* (striped). Based on Lindroth (1962), Turin *et al*. (1977), and personal observations.



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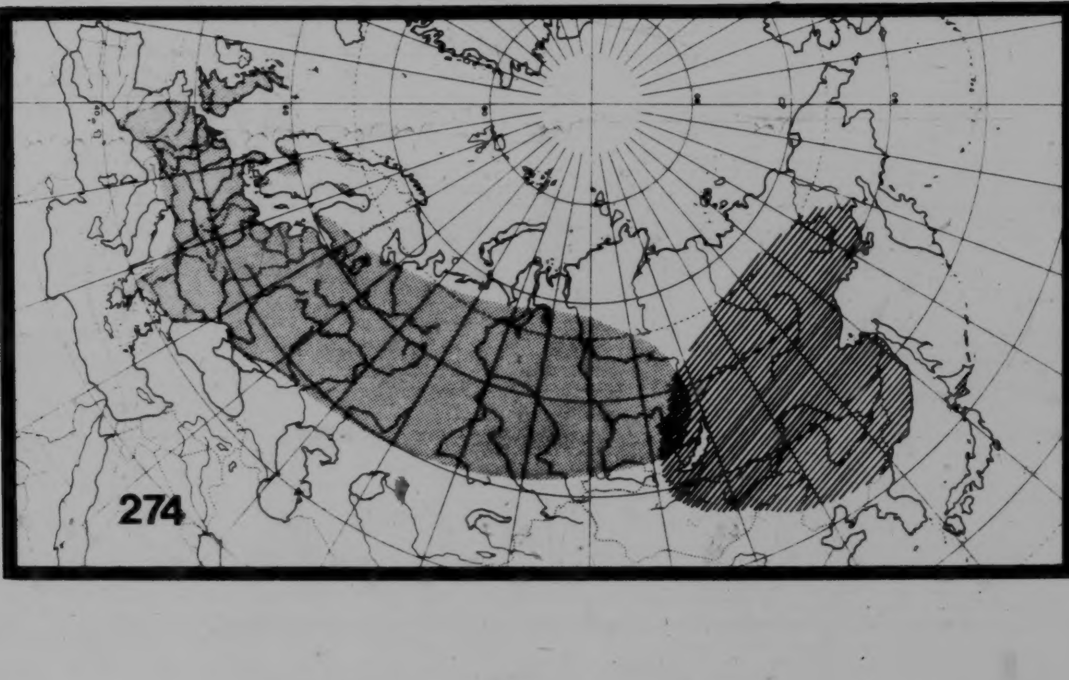

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Table 2. Character states in *Chrysobracteon*.

Species abbreviations: **bl**: *B. balli*, **fo**: *B. foveum*, **ar**: *B. argenteolum*, **al**: *B. alaskense*, **sm**: *B. semenovi*, **st**: *B. stenoderum*, **ca**: *B. carinula*, **vx**: *B. velox*, **lp**: *B. lapponicum*, **pn**: *B. punctatostriatum*, **hs**: *B. hesperium*, **lq**: *B. lorquinii*, **ze**: *B. zephyrum*, **lvl**: *B. levettei levettei*, **lvc**: *B. levettei carrianum*, **in**: *B. inaequale*, **lt**: *B. litorale*, **bk**: *B. baikaloussuricum*.

Other symbols: **"a/b"**: state intermediate between state **a** and state **b**; **"a,b"**: taxon dimorphic, with both states **a** and **b**; **"a-c"**: taxon polymorphic, with states **a** through **c**; " - ": character not applicable; " . ": character state unknown.

Number of specimens examined for each datum listed in Table 9.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	bk
Adult																		
Microsculpture																		
1.mirrors on interval 3 0-absent 1-very slightly shinier 2-slight mirrors 3-distinct mirrors	1	1	3	3	2	3	3	3	3	3	2,3	3	3	3	3	3	3	3
2.mirrors on intervals 4 or 5 0-absent 1-very slightly shinier 2-slight mirrors 3-distinct mirrors	1	1	2,3	2,3	2	3	0-2	0-2	0-3	0-2	3	3	3	3	3	3	3	3
3.mirrors on intervals 6 or 7 0-absent 1-very slightly shinier 2-slight mirrors 3-distinct mirrors	0	0	0,1	0	0	2,0	0	1	0,2	1	2,0	1	2,3	3	3	3	3	3
4.interval 7 mirror isolated? N-no Y-yes	-	-	-	-	-	N	-	-	N	-	N	-	N	N	N	Y,N	Y,N	N,Y
5.silver spot on interval 4? N-no, restricted to 3rd Y-yes	N	N	N	Y,N	N	N	N	N	N	N	N,Y	Y,N	Y,N	Y	Y	Y,N	Y,N	N,Y
6.elytral sculpticell shape I-isodiametric T-transverse	I	I	I	I	I	I	I	I	I	I	T,I	I	I	I	I	I	I	I
Sensilla																		
7.suborbital setae 0-absent, Fig. 60 1-short and sparse 2-denser, Fig. 59	1,2	1,2	2	2	2	1,2	2	2	2	0	1	0,1	2	2	2	0-2	2	2
8.midlateral pronotal setae 0-absent	1	1	0	0	0	0	1	1	1	1	0	0	1	1	1	1,0	1,0	0

Table 2, *cont'd.*

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	bk
1-present																		
9. ed3 and ed5 - position relative to 3rd interneur **A**-attached to interneur **F**-"free", in interval	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F
10. ed3 and ed5 - position relative to silver spot **A**-anterior end of spot **C**-center of spot	A	A,C	A	C	A	A	A,C	A	A,C	A	A	A	C	A,C	A,C	A,C	C,A	A
11. # setae between eo4 & e05 (average number)	.05	.80	1.8	.10	4	0	.40	0	.09	2.1	0	.07	0	0	0	.04	0	.14
12. # setae ed7 area (average number)	1	1.1	.92	1	1	1.9	1	1	1.1	1	1	1	1	1	1	1	1	1
13. male adhesive setae **N**-narrow, Fig. 86 **W**-wide, Figs. 84-85	W	W	W	W	W	W	W	W	W	W	W	W	W	W	W	W	N	N
14. protarsomere 4 ventroapical setae **F**-apically flattened, wide, Fig. 96 **C**-less flattened, more circular, Fig. 94 **C***- as **C**, but homology of setae questionable	F	F	C	C	C	F	F	F	F	C	F	F	F	F	F	F	F	
15. protarsomere 4 setal separation **N**-narrow, Figs. 93-96 **W**-wide, Fig. 92 **W***- as **W**, but homology of setae questionable	N	N	N	W	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Head																		
16. mandible shape **C**-curved, Fig. 25 **S**-straight, narrow, Fig. 28	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
17. lacinia shape **C**-curved, Figs. 44-48 **S**-straight, narrow, Fig. 42	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
18. lacinia width **N**-narrow, Figs. 46-47 **W**-wide, Fig. 48	N	N	N	N	N	N	N	N	N	W	N	N	N	N	N	N	N	N
19. mentum tooth shape **T**-triangular, trapezoid	T	T	T	T	T	T	T	T	T	R	T	T	R	R	R	R	T	R

Table 2, *cont'd.*

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	bk
R-rectangular, with deep lateral incisions																		
20. mentum tooth emarginate? **N**-no **Y**-yes	N	N	N,Y	N,Y	Y	N	N	N	N	N	Y,N	Y	N,Y	N	N	N	Y	N,Y
21. mentum tooth bulbous? **N**-no **Y**-yes, Figs. 52, 55, 57	N	N	N	N	N	N	N	N	N	Y	N	N	N	Y	Y	Y	N	N/Y
22. mentum epilobes **0**-indistinct, Figs. 52, 55 **1**-distinct, Figs. 49-51	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	0	1	1
Thorax																		
23. pronotal shape **T**-trapezoid, prominent anterior corners **R**-rounded sides	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R
24. pronotal carina **0**-absent **1**-short, separated from base, Fig. 71 **2**-long, separated from base **3**-long, attached to base, Fig. 70	0,1	0,1	0,1	0	0	1	3	0,1	1	1,0	0,1	0,1	1,0	0,1	0,1	1,0	0	1,0
25. metasternum **U**-unbordered **B**-bordered	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
Elytra																		
26. elytral basal impression **0**-absent **1**-slight **2**-definite	2	2	0	0	0	0	2,1	0,1	1	0,1	2,1	2	2	2	2	0-2	2,1	1,2
27. angulate humeral margin **A**-absent **S**-short, Figs. 69, 73 **M**-moderate, Figs. 68, 70 **L**-long, Figs. 71, 72	S,M	S	M	S	M	L	M	L	L	L	S	S	S	S	S	S	S	S
28. interneur 4 shape **0**-straight **1**-slightly sinuate **2**-distinctly sinuate	0	0	0	0	0	0	0	0	0	0	0	0	0-2	0-2	2	2	2,1	0,1

Table 2, *cont'd.*

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	bk
29. elytra around ed3 and ed5 foveolate? **N**-no **Y**-yes	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
30. elytral punctures **T**-transversely stretched **C**-circular **C***-some specimens C, others C/T	C	C	C	C	C	C	C	C	C	C	C/T	C	C	C	C	C*	C	C
31. interneur 8 depth **S**-as shallow as 7th anteriorly **D**-distinctly deeper than 7th anteriorly **S***-some specimens S, others S/D	S	S	S	S	S	S/D	S	S	S	S	S	S	S	S	S	S*	S	S
32. interval 5 posteriorly **R**-ridged **F**-flat	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F
33. subapical elytral plica **0**-absent **1**-internal only, not connected to epipleuron **2**-connected to epipleuron	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
Legs																		
34. male protarsomere 3 shape **0**-no lateral projection, Figs. 75-77 **1**-slight projection **2**-prominent projection, Fig. 78	0	0	0	0,1	2	0	0	0	0,1	0	0	0	0	0	0	0	0	0
35. protarsomere 4 projection **A**-absent, minute, Figs. 90-94 **S**-short, Fig. 95 **L**-long, Fig. 96	L	L	A	A	A/S	L	L	L	S	A	S	S	S	S	S	S	S	S
Male genitalia																		
36. flagellar sheath **0**-as Figs. 112-113, 117-128 **0***-as 0, but with long, thin scales	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0

Table 2, *cont'd.*

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	bk
1-dark and hooked, Figs. 114-116																		
37. CSC right lobe **A**-absent **N**-present, ventral margin narrow **W**-present, ventral margin wide	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
38. CSC right lobe ridge **0**-no ridge **1**-slightly **2**-distinctly	0	0	0	0	0	2	0	2	2	0,1	0,1	2	0	0	0	0	0	0
39. VSP dorsal ridge **0**-not angled, Figs. 112-120 **1**-slightly **2**-sharply angled, Figs. 124-128	0	0	0	0	0	0	0	0	0	0	0/1	1	0/1	2	2	2	2	2
40. VSP dorsal ridge sculpture **0**-unscaled **1**-scaled	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0
41. dark spot on flagellar sheath **0**-absent **1**-present	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42. ostial microtrichial patch size **A**-absent **S**-small, Fig. 116 **M**-medium (not dorsal), Figs. 114-115 **L**-large, dense, dorsal, Figs. 112-113	L	L	M	M	M	S	M	L	L	L	L	L	L	L	L	L	L	L
43. ostial microtrichia **0**-comb-like scales absent **1**-combs few **2**-combs extensive **2***-combs extensive, sparse, small	2	2	0	0	0	0	0	0	1	0	0,1	0	2	0	0	0	0	0
44. ostial sclerotized strip **0**-absent, Figs. 123-124 **1**-present, Figs. 126-128 **1***-present, beaded	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
45. pillow with scales	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0

Table 2, *cont'd.*

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	bk
O-absent																		
1-present, Fig. 119																		
46. internal sac leftmost central membrane	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
S-small scales																		
L-large scales, Fig. 108																		
47. ventral bulge	0	0	1,0	1	0	0	0	0	0	0	0,1	0,1	0,1	0	0	2	0	0
0-absent																		
1-slight																		
2-distinct, Fig. 126																		
48. aedeagal apex	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
B-abruptly ventrally bent																		
S-straighter																		
Female genitalia																		
49. vaginal sclerotized plate	0	0	0	0	.	0	0	0	0	0	0	0	0	0	0	0	0	0
0-absent																		
1-present																		
50. spermatheca apically indented?	N	N	N	N	.	N	N	N	N	N	N	N	N	N	N	N	N	N
N-no																		
Y-yes																		
51. stylomere 1 setal length	M	M	M	M	.	L	S	M	M	M	M	M	M	M	M	M	M	M
A-absent																		
S-short, Fig. 154																		
M-medium																		
L-long, Fig. 152																		
52. stylomere 2 length (micrometers, average) *** *B. zephyrum* varies from 190 to 325 micrometers	168	171	361	310	.	154	410	194	188	198	219	174	***	186	169	158	190	167
53. #dorsolateral sensilla	2	2	2-4	3-4	.	2	4-6	1-2	1-2	2-3	0	1-2	1-3	2-3	2-3	1-2	2	2
54. sternum X setation	L	L	L	L	.	L	VS	L	L	L	L	L	L	L	L	L	L	L
VS-very short, nubbin-like																		
L-longer																		
Chromosomes																		
55. autosome number	22	22	.	22	.	.	22	.	22	22	20	20	20	20	20	20	.	.
56. Y chromosome size	L	L	.	S	.	.	S	.	L	L	M	M	L	.	M,L	M	.	.
A-absent																		
S-small, <$\frac{1}{3}$ autosome size																		
M-medium, $\frac{1}{3}$-1 autosome size																		
L-large, about autosome size																		

Table 2, *cont'd*.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	bk
Larva - first instar																		
Color																		
57. frontale 3-spotted?	Y	Y	N	N	.	.	N	.	N	Y	Y	Y	Y,N	Y	Y	Y	.	.
N-not distinctly																		
Y-yes																		
58. head (other than spots)	D	D	C	C	.	.	C	.	D	L	L	L	L	L	L	L	.	.
L-light																		
C-centrally dark																		
D-dark																		
Microsculpture																		
59. frontale behind FR_3	1	1	.	0	.	.	0	.	1	2	1	1	1	1	1	1	.	.
0-absent, Figs. 227-228																		
1-laterally only, Figs. 229, 231																		
2-centrally, Fig. 230																		
60. frontale - anteriorly behind FR_3	M/S	M	.	A	.	.	A	.	S	S	S	S	S	S	S	S	.	.
A-absent																		
M-some multitoothed combs																		
S-single-toothed denticles																		
61. parietal eggbursters	D	D	.	ST	.	.	LT	.	ST	D	D	D	D	D	D	D	.	.
D-small denticles, Figs. 226, 230-231																		
ST-small teeth, Figs. 227, 229																		
LT*-large teeth, spaced.																		
LT-large teeth, clustered, Fig. 228																		
62. pronotal microtubercles	1	1	.	0	.	.	0	.	2	4	0	0	0	0	0	0	.	.
0-absent																		
1-present only laterally																		
2-laterally, faint centrally																		
3-absent between $PR_{1,4}$																		
4-absent only before $PR_{1,4}$																		
5-prominent throughout																		
Sensilla																		
63. seta FR_1 width	N	N	.	N	.	.	W	.	W	N	N	N	N	N	N	N	.	.
N-<$\frac{1}{2}$ FR_2 width																		
W->$\frac{1}{2}$ FR_2 width																		

Table 2, *cont'd.*

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	bk
64. seta FR_3 width **N**-<$\frac{1}{2}$ FR_2 width **W**->$\frac{1}{2}$ FR_2 width	N	N	.	N	.	.	W	.	W	W	N	N	N	N	N	N	.	.
65. seta PR_4 length **S**-short, Fig. 241 **L**-long, Fig. 240	L	L	.	L	.	.	L	.	L	S	L	L	L	L	L	L	.	.
66. seta PR_{10} length **A**-absent **S**-short, Fig. 243 **M**-medium, Fig. 244 **L**-long, Fig. 242	L	L	.	L	.	.	S	.	L	A	L	L	L	L	L	L	.	.
67. gPR & gME lateral setae **O**-absent **1**-present, Figs. 237, 241	O	O	.	O	.	.	O	.	O	1	O	O	O	O	O	O	.	.
68. seta PR_{13} size **VS**-short **L**-long	L	L	L	L	.	.	VS	.	L	L	L	L	L	L	L	L	.	.
69. seta ME_2 length **VS**-very short, Fig. 246 **S**-short **M**-medium, Fig. 247 **L**-long, Fig. 248	L	L	.	L	.	.	VS	.	VS	S	L	L	L	L	L	L	.	.
70. seta ME_{14} length **VS**-very short **S**-short **M**-medium **L**-long	L	L	L	L	.	.	VS	.	L	L	L	L	L	L	L	L	.	.
71. seta TE_6 length **VS**-very short, Fig. 253 **S**-short, Fig. 254 **L**-long, Fig. 252	L	L	.	L	.	.	VS	.	VS	S	L	L	L	L	L	L	.	.
72. seta TE_{11} length **VS**-very short, Fig. 250 **S**-short **L**-long, Fig. 248	L	L	L	L	.	.	VS	.	L	L	L	L	L	L	L	L	.	.
73. seta TE_{11} shape **N**-narrow, parallel-sided, Fig. 249 **W**-basally wide, tapered, Fig 248	W	N	.	W	.	.	-	.	W	W	W	W	W	W	W	W	.	.
74. seta TEα (near TE_8) **O**-absent **1**-present, Fig. 251	O	O	.	O	.	.	O	.	O	1	O	O	O	O	O	O	.	.

Table 2, *cont'd*.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	bk
75. seta EP, length **S**-short, Fig. 251 **L**-long, Fig. 248	L	L	.	L	.	.	L	.	L	S	L	L	L	L	L	L	.	.
76. segment VIII seta EP, width **N**-$<\frac{1}{2}$ EP, width **W**-$>\frac{1}{2}$ EP, width	N	N	.	N	.	.	W	.	W	-	N	N	N	N	N	N	.	.
77. seta ST, on segment IX **0**-absent **1**-present, Fig. 256	0	0,1	.	0	.	.	1	.	1	0	0	0	0	0	0	0	.	.
Head																		
78. mandible mesal margin **0**-shelf absent, Fig. 200 **1**-narrow shelf, Fig. 199 **2**-wide shelf, Fig. 198	1	1	.	0	.	.	2	.	2	0/1	0	0	0	0	0	0	.	.
Larva - second instar																		
79. extra setae near FR, **0**-absent **1**-present	0	.	.	1	.	.	1	.	0	0	0	0	0	0	0	0	.	.
80. L, stipites **3**-3 outer setae **4**-4 outer setae	3	.	.	3	.	.	3	.	3	3	3	3	3	3	3	3	.	.
81. # long urogomphus setae see Figs. 258-260	7	.	.	7	.	.	10	.	9	7	7	7	7	7	7	7	.	.

5. PHYLOGENY OF *CHRYSOBRACTEON*

5.1 Methods

5.1.1 Principles of phylogeny reconstruction

In deciphering the course of biotic history, of primary importance is discovery of the pattern of splitting of lineages, and the manner in which traits have been passed along lineages. But breeding ties of past organisms cannot be observed directly, and so some secondary indicators of genealogical relationship must be sought. The only evidence we have for a group such as *Chrysobracteon* is that provided by the characteristics of living species; the few *Chrysobracteon* fossils offer little help.

The hypotheses of phylogenetic branching pattern and character state evolution to be chosen for a group such as *Chrysobracteon* are those that best explain the diversity in extant organisms. This may seem straight-forward, but it is not: the various interpretations of "those that best explain the diversity" have been the subject of a great deal of controversy. Two of the most crucial issues involved in the controversy are included in the debate between Felsenstein (1982, 1983) and Farris (1983). One issue involves scientific methods: should our inferences be based upon a deductive-logic-and-parsimony approach to science, or a probabilistic approach? The second is much more provincial: what assumptions about evolution should we begin with at the start of the analysis?

I am ill-adapted to deal with the first question now. It appears to me that if one wishes to make probabilistic claims about the phylogeny or include probabilistic background assumptions, then a likelihood (or at least a statistical) method is necessary. If one does not wish to make probabilistic claims about the cladogeny, and one does not accept probabilistic process hypotheses, then a deductive-logic-and-parsimony approach is the only possible scientific method. However, I can only vaguely see some of the subtleties involved in a general choice between the methods, and I will leave this problem for now.

Whatever methods and background assumptions we might choose, there are a few common features of any attempt at phylogeny reconstruction.

First, it is a fact of cladistic inference that *any* phylogenetic branching pattern can be used to fully explain *any* pattern of diversity, if one hypothesizes the appropriate character evolution. Thus, we cannot simply choose the *most* explanatory phylogenetic tree; all tree hypotheses can be as explanatory. Also, unless one has some initial preference for, say, symmetrical trees, one cannot choose among phylogenetic branching patterns on the basis of the branching patterns themselves; rather, one must look to the nature of the hypotheses of character evolution, and judge the phylogeny on that basis. Techniques of phylogenetic reconstruction therefore compare hypotheses of character evolution.

Second, it is important that we strive to make our hypotheses of character evolution and phylogeny to be the "best explanatory hypothesis" not just in isolation but also within a broader framework. We have to consider them in the context of hypotheses about related groups and of established notions about genetics, development, evolutionary ecology, etc. That is, we must make sure that we choose hypotheses for our study group ("ingroup") that allow for "good" hypotheses of related group ("outgroup") evolution; we do this by using some form of outgroup analysis. We must also make sure our hypotheses are consistent with our background assumptions about evolutionary rates, developmental constraints, etc. This striving for compatability of our hypotheses with the rest of biology is important whatever our phylogeny reconstruction methods might be. But which background assumptions are justifiable?

Several authors (among others, Eldredge and Cracraft (1980), Patterson (1982)) have claimed that we should not include *any* background assumptions about evolution (or, at most, only that it has occurred), that we should reconstruct the cladistic history of life without reliance on preconceived notions of evolutionary processes. Some of these authors would have us use a technique such as Wagner analysis (Farris 1983), which supposedly does not require evolutionary process hypotheses for justification, to choose an hypothesis of phylogeny.

Eldredge and Cracraft (1980) state that one mustn't use hypotheses of evolutionary process in reconstructing phylogenetic patterns, as one must separate pattern from process. One primary reason for this separation is to avoid circularity. This is not, however, a sufficient reason to always separate pattern from process. Its desirability depends upon our goals, upon the use to which one wishes to put the phylogenetic pattern. If one wishes to use the pattern to test an hypothesis of process, then one must not uncautiously use that process hypothesis to construct the pattern, for fear of unrecognized bias and circularity. Such testing of evolutionary process hypotheses using systematic results is valuable, and retesting will always be worthwhile as biology grows. The relatively recent advances in phylogenetic inference (most notably Hennig's (1966) insights) give us new tools with which to retest hypotheses of evolutionary processes. But we needn't always be in the business of testing such process hypotheses. Indeed, if one wishes an hypothesized phylogeny for its own sake or as a basis for biogeographic or ecological studies, for example, the use of established evolutionary processes is warranted if not required.

But what are "established evolutionary processes?" At least some evolutionary processes are already fairly well documented, and can be used with some degree of confidence. A quite general law, accepted by most systematists, is that the taxic diversity we see among animals arose by evolution within predominantly dichotomizing lineages, and, *all else being equal enough*, we would then expect that if a pattern in distribution of character states exists, it would be a hierarchically nested pattern. This notion of diversifying evolution is a general biological law that is itself supported by evidence from other organisms.

Other than these most general laws, however, acceptable hypotheses about evolutionary processes are subject to more debate and less agreement. These "lesser laws" of relevance to phylogeny reconstruction can be of several sorts. They can propose relative likelihood of evolutionary changes between states of one character, or the relative rates of evolution of two or more characters, or the interactions between evolution of two or more characters, or the interactions between various lineages of the taxon, or interactions between members of the taxon and the environment.

For example, likely evolutionary pathways within a taxon can sometimes be inferred from observations made on other groups. It seems clear that in groups containing both cave-adapted and above-ground species, the cave-adapted forms are derived. This hypothesis can be supported by outgroup analysis on a large number of groups, and by accepted hypotheses about developmental and ecological constraints. Lineages that shift habitat into caves have a tendency to loose eyes, and pigmentation, often with associated lengthening of body appendages. A process such as this, documented in some groups, can be used as a general evolutionary law, which can then be applied in another group. For example, if one were to discover a group containing a few depigmented, eyeless, cave-dwelling forms, as well as pigmented, eyed, above-ground forms, the cave-dwelling forms can be presumed to be derived.

A "group trend" (Ross 1974) hypothesis such as this is supported by both phylogenetic analysis of a number of groups as well as mechanistic (ecological, developmental, or genetic constraint) explanations about the reasons for the unidirectionality of evolution. If for another group-trend hypothesis, however, the mechanistic supporting hypotheses are lacking, and the trend hypothesis is based only on other reconstructed phylogenies, then evidence for the universality of the hypothesis is weaker; indeed, Farris (1983) would not accept such hypotheses. On the other hand, only ecological, developmental, or genetic studies done on living populations might support another evolutionary process hypothesis; when would such an hypothesis be acceptable? In general, it is unclear how much evidence from which sources is needed before an hypothesis of evolutionary process is to be accepted for use in phylogenetic analysis. Perhaps the most important message to come out of the "theory-free" cladistics of Platnick (1979) and others is that we must not uncritically accept process hypotheses for use in every phylogenetic analysis attempted; indeed, we should accept only those process hypotheses that pass a scrupulous examination. Those that I have accepted and included within my analysis will be discussed as required.

5.1.2 Techniques of phylogeny reconstruction

The diversity of opinions about principles of phylogenetic reconstruction has spawned a myriad of methods. Most of the methods follow a common procedure, consisting of:

(1) delineation of characters and character states;
(2) hypothesizing transformation networks;
(3) synthesis of transformation networks and the distribution of character states.

At some point in the procedure, species must be delimited. Those who prefer species to be minimally monophyletic units may do this during step three; I begin it before step one (see "Species and subspecies recognition" section, p. 75).

Some systematists, especially paleontologists, would include in the synthesis of step three information about temporal distribution of fossils, and perhaps known events in the environment's past (formation of epicontinental seas, ice ages, abundance of conifers, and so on). I have not included such information in my analysis.

Delineation of character state sets (characters)

Methods for reconstructing phylogenies begin by hypothesizing sets of homologous states. The goal is proposal of characters each consisting of a set of states of which one state, and only one, would likely occur in each organism. Positional, developmental, and genetic criteria are used to divide the organism. Characters are chosen so that the states have some common genetic basis; this makes simpler the job of proposing likelihood or simplicity of evolutionary change.

I will not discuss the homology issue more here; the reader is referred to works such as Hecht and Edwards (1976), Wiley (1981), and Patterson (1982).

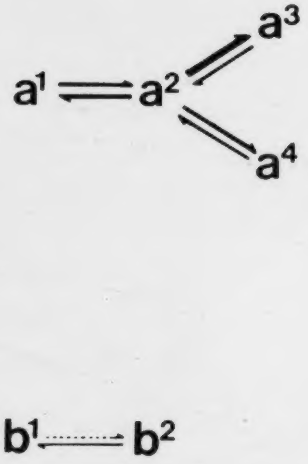
Hypothesizing transformation networks

Once a character has been delimited, and its states defined, then these states are linked into an undirected or directed tranformation network. Linking states may be as simple as proposing that evolution went from **A** to **B** (or the reverse) [that is, the transformation series is **A↔B**], or as complex as proposing a full set of connections between any two states of a ten-state character.

These connections need not be equally strong; they can be weighted with respect to each other. For example, in Fig. 275, the thickness of an arrow connecting states represents either a measure of simplicity of hypothesis of transition (if a pure deductive-logic-and-parsimony approach is taken), or of probability of transition (if a likelihood approach is

Figure 275. Two examples of transformation networks. The thickness of the arrows is proportional to the simplicity of hypothesis of character state change or the probability of character state change. Different thicknesses of the arrows within a character transformation network (*e.g.* the $a^2 \rightarrow a^3$ arrow versus the $a^2 \leftarrow a^3$ arrow) indicates intra-character weighting; between transformation networks (*e.g.* the $a^1 \rightarrow a^2$ versus $b^1 \rightarrow b^2$ arrows), inter-character weighting.

2


a^1
a^2
a^3
a^4
b^1
b^2

275

used). A measure of simplicity of hypothesis of transition would be based on the phenetic (or preferably genetic) difference between states of a character. For example, if two character states are quite different, both phenotypically and in the underlying genes, then the value accorded that branch on the transformation network would be high. The probability of transition would be proposed on the basis of background hypotheses about the nature of the evolutionary process.

These measures of the relative simplicity of hypotheses or likelihood of transition between states of a character can be considered *intra-character weighting*. Similarly, the differences between these transition measures for different characters I term *inter-character weighting* (see Fig. 275).

One may decide that intra-character or inter-character weighting may not be invariant throughout the analysis: they may be conditional on the "environment" of the character, as characters do not evolve independently. For example, consider the evolution of metathoracic wings in insects. The initial transition of lack of wings to presence of metathoracic wings would be given a high weight, as it involves the buildup of a presumably large number of coordinated genes. But the reverse transition, loss of wings, could be given a low weight, as it could be accomplished by the simple action of a regulatory gene. However, these intra-character weightings would change for groups whose ancestors had wings; for these, loss *or* gain of wings could presumably be accomplished rather readily by a switch in regulatory genes.

Another example comes from *Chrysobracteon*. Mirror diversity in the subgenus is documented by three characters (mirrors (1) on interval 3, (2) on intervals 4 and 5, and (3) on intervals 6 and 7). It may be true that once mirrors have formed on one interval, subsequent spread of mirrors to other intervals will be easier than initial evolution of mirrors on those intervals. If so, then the weights of these mirror characters will drop for any clade in which some mirrors have arisen.

The example of wing evolution illustrates a change in thinking about character weighting. Advances in genetics, especially regarding regulatory genes and epigenetics, have shown that small genetic changes can have rather drastic phenotypic effects; conversely, canalization can yield similar phenotypes from different genotypes. The connection between magnitude of genetic and phenotypic differences seems to be more tenuous than formerly believed, and thus it is a dubious business to base intra-character or inter-character weightings on phenotypic differences. Because for most groups genetic differences are not known directly, weightings, by necessity based on phenotypes, should perhaps be viewed with more skepticism. In the past, before knowledge of regulatory genes and epigenetics, weighting was a more reasonable enterprise. Even D. Sharp's (1903) extreme weighting of metathoracic wing length in carabids (he placed long- and short-winged specimens in different genera) seems not so absurd in the context of the times.

I think the safest way to proceed with respect to weighting is to begin with characters unweighted (that is, intra-character and inter-character weights all equal), and then alter the weights only where there is good reason to do so. (Kluge and Farris (1969) and others have expressed a similarly cautious view of weighting.) Weighting that I used will be discussed with my analysis.

Synthesis of transformation networks and character state distributions

These transformation network hypotheses, whether they be hypotheses of simplicity of change or probability of change, one for each character, are then combined with the character state distribution across taxa, and any cladistic structure accepted *a priori*, to form the basis of phylogeny inference. Exactly how this is done will depend upon the accepted hypotheses about the nature of evolution. Two rigorously defined numerical methods of phylogenetic inference, Wagner analysis (a deductive-logic-and-parsimony method) and Maximum Likelihood Estimation (a statistical method), can serve as clear examples of two major approaches. After outlining these approaches to the synthesis, I discuss non-numerical techniques of mental argument.

Wagner analysis.- If one prefers not to accept hypotheses about likelihood of evolutionary direction or change, and begins a study with a neutral position regarding likelihoods of change, then some non-probabilistic reconstruction technique, justified non-statistically, will be necessary. Farris (1983) and Sober (1983a) have used the philosophical criterion of parsimony of hypotheses to support Wagner analysis and related procedures.

Wagner analysis attempts to find the tree for which the hypothesis of required character state change is simplest; that is, the tree requiring the minimum number of *ad hoc* hypotheses of homoplasy (Farris 1983). This tree is called the most parsimonious or Wagner tree. If outgroups are adequately resolved, then the hypothesis of ingroup cladistic structure that is most parsimonious in the context of the outgroups (*i.e.* globally most parsimonious) can be obtained by including the outgroups, their cladistic structure, and their character states in the analysis. ("Globally" is used here in its mathematical sense, that is: pertaining to the full set of considered objects, not just a portion thereof; in contrast to "locally": pertaining to a portion of the full set of considered objects. In my study, the full set of considered objects includes all species of Tables 2, 4, and 5, and all characters listed therein.) An equivalent technique uses the outgroup algorithm of Maddison *et al.* (1984) to hypothesize ancestral states which are then used in conjunction with Wagner analysis on the ingroup.

(Algorithm is a noun meaning: a set of step-by-step rules for solving a problem, such as discovery of ancestral states.) If outgroups are inadequately resolved, then the globally most parsimonious hypothesis can be obtained in a similar fashion, with the outgroups being resolved simultaneously with the ingroup.

At least in theory, Wagner analysis can incorporate a full range of character types with intra- and inter-character weighting. This will allow for the phylogenetic hypotheses to be parsimonious not only with respect to evolution in outgroups, but also in the context of accepted hypotheses of evolutionary process. It is thus not restricted to simple character-step counting.

This point cannot be overemphasized. Parsimony is not a restrictive assumption used only by systematists seeking theory-free phylogenetic hypotheses. It is a general working principle within science, and is to be used with all kinds of hypotheses. And it need not lead to simple hypotheses; as Sober (1983b) states, the parsimony "criterion places no upper bound on how complex nature might be".

There are several available computer programs that search for the Wagner tree; three widespread program packages are Farris's PHYSIS, Felsenstein's PHYLIP, and Swofford's PAUP.

Maximum Likelihood Estimation.– Felsenstein's (1981, 1982) maximum likelihood estimation requires some probabilistic hypothesis about evolutionary rates. He has shown that under one simple model of evolution with low rates of evolution in all characters, Wagner analyses (with characters weighted in accordance with the logarithms of their rates of change) generate the tree of maximum likelihood. When evolutionary rates are small enough, unweighted Wagner methods produce maximum likelihood estimates. If a few characters evolve rapidly, and the rest very slowly, but it is not known which characters evolve quickly, then compatibility analysis (Estabrook *et al.* 1977, Felsenstein 1982) is the appropriate maximum likelihood technique. Sober (1983a) argues that under an even more general model of evolution, parsimony techniques *always* generate most likely cladograms. However, his argument does not guarantee that Wagner trees will be maximum likelihood estimates (D.R. Maddison, unpubl.). Further studies of maximum likelihood estimates under different models and rates of evolution may be one of the most fertile areas of study in numerical phylogenetics, especially if relatively robust, relatively non-parametric models such as Sober's can be shown to produce powerful maximum likelihood estimating procedures.

Felsenstein has available a computer program, PHYLIP, designed to find the maximum likelihood estimate of the phylogenetic tree under some simple evolutionary models.

Non-numerical techniques.- Many of the non-numerical approaches used by systematists are essentially less-rigorous versions of maximum likelihood estimation, or a parsimony approach, or an amalgam of the two. The rigorous portions of these mental techniques are by necessity shorter and less complex than those used in computers, and, as expected, they are therefore less powerful. The non-rigorous portions make up for some of this lack of depth by allowing inclusion of more information in the analysis. However, these non-rigorous, more intuitive portions of the method lack openness to critical examination. The hypotheses they produce are open to critical examination, as are all hypotheses, but the methods are not.

Of the non-numerical methods currently used for inferring the phylogeny of a group of organisms, almost all involve an initial assessment as to which states of a character were present in an ancestor of the ingroup. This initial assessment indirectly leads to hypotheses of derived and ancestral states within the ingroup, which aid in tracing the evolution of the character through the group. These hypotheses can then be used to corroborate the monophyly of subgroups that possess derived states (Hennig 1966; Wiley 1975). Two steps are thus involved: initial hypothesizing of ancestral states, and resolution of the ingroup. Techniques for resolution of the ingroup itself can involve hypothesizing ancestral states of a part of the ingroup, and thus some of the same procedures can be used for both steps.

I refrain from using the term "character polarization" for hypothesizing ancestral states, as a procedure such as

Maddison *et al.*'s (1984) outgroup analysis does not directly hypothesize states derived within the ingroup, and thus it does not provide an initial polarization of character state evolution within the ingroup. At most they provide polarization within the ingroup and the ingroup's stem group (the stem group being the outgroup - ingroup internode, Maddison *et al.* 1984). To presume otherwise would overly restrict the proposed character evolution (see Maddison *et al.* 1984).

Methods proposed for inferring which states are ancestral (or which derived) are numerous, and have been reviewed by Crisci and Stuessy (1980), de Jong (1980), Stevens (1980), Arnold (1981), and others. The three methods most widely discussed today are outgroup analysis, the ontogenetic method, and the paleontologic method. The debate in the literature on the relative merits of these techniques, carried on by Nelson (1978), Patterson (1982), Voorzanger and van der Steen (1982), and Maddison *et al.* (1984), among many others, is unfortunately nearly irrelevant for ground beetle systematics: the ontogeny and fossil record of carabids are so poorly known that the methods are for the most part inapplicable. This is certainly true for *Chrysobracteon*.

Several techniques have been used recently by students of beetles (see, for example, Ball 1975, 1978; Ball and Shpeley 1983; Ekis 1977; Goulet 1983; Kavanaugh 1978; Erwin and Kavanaugh 1981). Some of these techniques, such as the use of group trends, are methods of intra-character weighting, not based on the distribution of character states. I have already discussed these under "Hypothesizing transformation networks". Other techniques use the distribution of character states across taxa, and these I will now discuss.

The names of techniques using character state distribution vary from author to author, with "outgroup analysis", "ingroup analysis", "character correlation" having several meanings each. I will sort through some of the diversity. At the same time I will discuss means of ingroup resolution.

Outgroup analysis involves choice of an hypothesis of ancestral state based on the distribution of character states in related organisms. A number of such procedures have been proposed (see Watrous and Wheeler 1981, Maddison *et al.* 1984). A technique of argument designed to approximate or discover the Wagner tree involves outgroup analysis *sensu* Maddison *et al.* 1984.

When outgroups are cladistically adequately resolved, the character states of the most recent common ancestor of the ingroup plus its sister group are estimated *via* an outgroup algorithm (Maddison *et al.* 1984), and then a second step of resolving the ingroup assuming those ancestral states is taken. Rigorous techniques of argument for this second step are more or less undeveloped, although Watrous and Wheeler's (1981) functional outgroup / functional ingroup routine (equivalent to Kavanaugh's (1978) "character correlation" method and Clark's (1978) "ingroup analysis") is a useful, albeit imperfect, method of Wagner-tree searching (see Maddison *et al.* 1984 for some of its problems).

However, when outgroups are imprecisely resolved, the outgroups and ingroups must be resolved simultaneously to guarantee the globally most parsimonious ingroup cladogram. One could imagine doing this mentally, by a reciprocal illumination technique that would entail resolution of part of the ingroup, then part of the outgroup, then a portion of the ingroup, and so on, until all the data provided by the characters were used. Such a technique has not been rigorously developed, and even if it were, it would probably suffer from some of the same problems as the functional outgroup / functional ingroup approach. Nonetheless, it may be the best we could do without lengthy calculations best done by a computer. Further discussion of the relationship between techniques of argument and the globally most parsimonious cladogram is given by Maddison *et al.* (1984).

The use of the outgroup analysis procedure of Maddison *et al.* (1984) followed by a mental parsimony-based ingroup resolution procedure will encompass a search for the Wagner tree. It might thus seem to be simply a non-numerical version of computerized Wagner analysis, with less hope of successfully finding the Wagner tree. However, it does have the advantage over available Wagner-tree searching programs in that it is not bound by restrictions in the types of characters used, the nature of their intra-character weighting, nor assumptions such as independence of character evolution.

Two other techniques for hypothesizing ancestral state are less clearly relatable to Wagner analysis: generalized outgroup analysis, and character correlation.

Generalized outgroup analysis is an amalgam of techniques, applied when outgroup relationships are inadequately resolved or "appropriate" outgroups are unavailable (Ball 1978, Ball and Nimmo 1983). It includes an examination of the distribution of character states in related groups, with exclusion of outgroups possessing a number of derived features. I prefer to consider this latter addition as application of the separate technique of character correlation, discussed later. Rather than proposing the most parsimonious hypotheses of ancestral state based on the cladistic structure and character state distributions (using an outgroup algorithm such as that described by Maddison *et al.* 1984), a simpler rule is used, that of proposing that the most widespread state (among generally primitive taxa) is primitive. Unfortunately, this simpler rule is not justified by parsimony considerations, except under special circumstances (Stevens 1980, Farris 1982, Maddison *et al.* 1984). Its results will match those of the outgroup procedure of Maddison *et al.* (1984), and therefore be justified by parsimony, only if there is enough cladistic structure in the outgroups for the outgroup procedure to yield a decisive ancestral state assessment of the most common state. This would occur, for example, if all outgroup taxa shared the same state. If this cladistic structure is not known, if the outgroups are inadequately resolved, then the outgroup procedure may not yield a decisive answer and the simple rule of presuming the widespread state is primitive will not be justified by parsimony. For example, in *Bembidion* other than *Chrysobracteon*, three states of character 1 (presence of mirrors on elytral interval 3; Table 2) occur in the outgroups (Table 5). While lack of mirrors (state 0) is most common among outgroup species, it would not be the most parsimonious choice of a *Chrysobracteon* ancestral state if groups such as *Ochthedromus* reveal themselves as the sister groups of *Chrysobracteon*. Rather than hypothesizing that the primitive state is the widespread one, and not knowing whether or not the hypothesis is supported, I suggest using the outgroup procedure of Maddison *et al.* (1984) to determine directly which hypotheses (if any) are supported by parsimony considerations.

In some instances, no specific hypothesis of ancestral state will be demonstratably most parsimonious. This may result in some taxa being phylogenetically undecipherable at present, unless some other technique such as application of group trends leads to resolution of the ingroup. But even this may not work, and the ingroup may remain incompletely resolved. This should not spur one to use a widespread-is-primitive rule to resolve the ingroup: I think that it is better to say nothing than to propose hypotheses supported only by unjustified techniques. It would be more productive to work on resolving the higher-level outgroup phylogeny, so that the ingroup may eventually be resolvable, or be satisfied with an unrooted or partly resolved phylogeny of the ingroup.

Use of *character correlations* has been advocated by Ekis (1977) and Hennig (1966) (and Kavanaugh (1978) under the name "correlation with adaptive significance") to infer character polarity. The method involves proposing relative apomorphy within one character to be of the same pattern as for another previously polarized character with correlated state distributions. The method is not clearly defined as stated, and thus it is not easy to evaluate. Ball (1975) and Kavanaugh (1978) use the term "ingroup analysis" for a similar procedural rule: the state associated with the phenotypically most plesiomorphic taxon is itself most plesiomorphic. In some instances, it will yield the same results as functional outgroup / functional ingroup procedures, and to that extent the rule seems acceptable. Otherwise, I see no justification for it. Its only support independent of the other methods of polarization would appear to be a general law that mosaic evolution is rare, and that characters tend to evolve in concert, producing animals composed mostly of plesiomorphic states, and others mostly of apomorphic ones, but with very few mixtures. The same general law is needed to justify ignoring sister groups possessing a number of derived features, as may be done in generalized outgroup analysis. As a general law this seems unsupported, and in fact often false, although it needs to be rigorously tested. Until such tests have been conducted, I would avoid the use of character correlation techniques.

Both generalized outgroup analysis and character correlation can be followed by the same techniques of ingroup resolution as is outgroup analysis *sensu* Maddison *et al*. (1984). As mentioned earlier, mental ingroup resolution has not been extensively studied. Rather than presenting a general discussion of the topic, I will simply describe the technique I used, within the following sections.

5.1.3 Methods used herein

I intended to use both mental cladistics, as well as the Wagner-tree searching programs of D. Swofford's PAUP. As I have only recently been able to get PAUP to function on the University of Alberta computers, I have restricted the present analysis to mental cladistics. In the published version of my work, I will include several numerical Wagner analyses performed by PAUP and synthesize these results with my mental results.

I have used a parsimony approach; that is, I attempt, mentally, to discover a tree similar to the Wagner tree, and present that tree as the reconstructed phylogeny. I weight some characters and perform an extensive outgroup analysis, using the outgroup algorithm of Maddison *et al.* (1984). I discuss the weighting scheme now, but include the description of those aspects of the method that involve character-state distributions (for example, outgroup analysis) within the analysis that follows.

In choosing evidence for my cladistic analysis, I have discarded about 50 characters after preliminary investigation. Characters eliminated were those that proved: (1) to be too difficult to interpret states of a given specimen without resorting to expensive SEM or other excessively time-consuming work; (2) to have too much variation within species, requiring much more time to document accurately than was available. After this pruning, 81 characters remained. Table 3 presents some information about each of these characters.

I weighted these characters in only a few circumstances. I saw no reason to alter intra-character weights from equality, with one major exception. All multistate characters whose traits were considered as ordered in a transformation series (those with an "O" under "type" in Table 3) were, of course, weighted simply by the ordering: a 0↔1↔2 tranformation series implies that a 0↔2 change is of greater weight than a 0↔1 change. I did not, however, use group-trend hypotheses, or assumptions such as irreversibility or loss-is-easier-than-gain. Too little is known or can be inferred about genetics of *Bembidion* characters to warrant use of such assumptions.

Similar biological assumptions that could be used for inter-character weighting were generally ignored. I should note that this near-equality of inter-character weighting is somewhat artificial, as some of the characters are weighted more than others simply by the way I coded the characters. I divided some characters into two states (say 0 and 1), others into three (say A, B, and C); the characters with more states are naturally weighted more highly than the ones with less, but this does not necessarily reflect greater genetic diversity requiring higher weights. Without knowing a considerable amount more about *Bembidion* than is known, I cannot tell if the genetic gap between 0 and 1 is any more or less than that between A and B or A and C. However, in the face of ignorance, I think that this (somewhat questionable) equality of weights is the best that can be done.

As well, weight of a character was decreased by about 20% in each of two circumstances: (1) it was subject to taxonomist's error, that is, I was doubtful about my ability to distinguish character states consistently or I felt my sample sizes were too low; (2) it was polymorphic in at least two species. The rationale for the latter decrease is that characters for which polymorphisms are maintained are less reliable phylogenetic indicators (see Kluge and Farris 1969, Hecht and Edwards 1976); this is the only hypothesis of evolutionary process I have used in my initial analysis. The weights thus obtained are indicated in Table 3 under "basic weight". The weights "0.6", "0.8", and "1.0" were not used exactly in the mental analysis; rather, they provided only a rough relative weighting of characters.

For one analysis, I decreased character weight if it belonged to a group of dependent characters; that is, characters belonging to the same genetic or functional group, and thus presumably evolving together. Dependent characters, if evolving completely in concert, should be given a weight of the inverse of the number of characters in the dependency group. As evidence for dependency is not profuse, I decided against such extreme weighting, and compromised, lowering such characters' basic weight by a fraction that was the average of an independent character and a fully dependent character, that is, by (1+[1/(number of characters in dependency group)])/2. These "altered weights" are listed in Table 3.

Table 3. Information about characters studied.

# states: numbers refer to number of discrete states; "C" means character values are continuous.

type: refers to character type, whether states are unordered ("U"), ordered ("O") into a linear transformation series, or arranged in a branched character state tree ("T"); binary characters are omitted. For the only character with a branched character state tree, 43, the tree is 0↔1↔(2 or 2*).

my errors: characters for which I had difficulty distinguishing states or for which I believe my sample sizes were too small are marked with an "X".

polymor. w/in species: characters polymorphic within at least two species are marked with an "X".

basic weight: the inter-character weightings, not including alterations to weights because of membership in a dependency group. See text for method of calculation.

dependency groups: all characters sharing a number in this column may belong to a group of evolutionarily-dependent characters.

altered weight: the inter-character weightings, including alterations to weights because of membership in a dependency group. See text for method of calculation.

Character	# states	type	my errors	polymor. w/in species	basic weight	dependency groups	altered weight
1.mirrors interval 3	4	O	.	.	1.0	1	0.6
2.mirrors on intervals 4 or 5	4	O	.	X	0.8	1	0.5
3.mirrors on intervals 6 or 7	4	O	.	X	0.8	1	0.5
4.interval 7 mirror isolated?	2	.	.	X	0.8	1	0.5
5.silver spot on interval 4?	2	.	.	X	0.8	.	0.8
6.elytral sculpticell shape	2	.	.	X	0.8	3	0.6
7.suborbital setae	3	O	X	X	0.6	.	0.6
8.midlateral pronotal setae	2	.	.	X	0.8	.	0.8
9.ed3 and ed5 - position relative to interneur 3	2	.	.	X	0.8	.	0.8
10.ed3 and ed5 - position relative to silver spot	2	.	X	X	0.6	.	0.6
11.# setae between eo4 & eO5	C	O	.		1.0	.	1.0
12.# setae ed7 area	C	O	.		1.0	.	1.0
13.male adhesive setae	2	.	.	.	1.0	.	1.0
14.protarsomere 4 ventroapical setae	2	.	X	.	0.8	2	0.5
15.protarsomere 4 setal separation	2	.	X	.	0.8	2	0.5
16.mandible shape	2	.	.	.	1.0	4	0.6
17.lacinia shape	2	.	.	.	1.0	4	0.6
18.lacinia width	2	.	.	.	1.0	4	0.6
19.mentum tooth shape	2	.	.	.	1.0	4	0.6
20.mentum tooth emarginate?	2	.	.	X	0.8	4	0.5
21.mentum tooth bulbous?	2	.	.	.	1.0	4	0.6
22.mentum epilobes	2	.	.	.	1.0	4	0.6
23.pronotal shape	2	.	.	.	1.0	.	1.0
24.pronotal carina	4	O	.	X	0.8	.	0.8

Table 3, *cont'd.*

Character	# states	type	my errors	polymor. w/in species	basic weight	dependency groups	altered weight
25.metasternum	2	.	.	.	1.0	.	1.0
26.elytral basal impression	3	O	X	X	0.6	.	0.6
27.angulate humeral margin	4	O	X	X	0.6	.	0.6
28.interneur 4 shape	3	O	.	X	0.8	.	0.8
29.elytra around ed3 and ed5 foveolate?	2	.	.	.	1.0	.	1.0
30.elytral punctures	2	.	.	.	1.0	3	0.8
31.interneur 8 depth	2	.	X	.	0.8	.	0.8
32.interval 5 posteriorly	2	.	.	.	1.0	.	1.0
33.subapical elytral plica	3	U	.	.	1.0	.	1.0
34.male protarsomere 3 shape	3	O	X	X	0.6	.	0.6
35.protarsomere 4 projection	3	O	X	.	0.8	2	0.5
36.flagellar sheath	3	U	X	.	0.8	9	0.4
37.CSC right lobe	3	O	.	.	1.0	5,9	0.4
38.CSC right lobe ridge	3	O	X	X	0.6	5,9	0.2
39.VSP dorsal ridge	3	O	.	.	1.0	9	0.5
40.VSP dorsal ridge sculpture	2	.	.	.	1.0	9	0.5
41.dark spot on flagellar sheath	2	.	.	.	1.0	9	0.5
42.ostial microtrichial patch size	4	O	.	.	1.0	9	0.5
43.ostial microtrichia	4	T	X	X	0.6	9	0.3
44.ostial sclerotized strip	3	U	.	.	1.0	9	0.5
45.pillow with scales	2	.	.	.	1.0	9	0.5
46.internal sac leftmost central membrane	2	.	.	.	1.0	9	0.5
47.ventral bulge	3	O	X	X	0.6	9	0.3
48.aedeagal apex	2	.	.	.	1.0	9	0.5
49.vaginal sclerotized plate	2	.	.	.	1.0	10	0.6
50.spermatheca apically indented?	2	.	.	.	1.0	10	0.6
51.stylomere 1 setal length	4	O	.	.	1.0	10	0.6
52.stylomere 2 length	C	O	.	.	1.0	10	0.6
53.#dorsolateral sensilla	7	O	.	X	0.8	10	0.5
54.sternum X setation	2	.	.	.	1.0	10	0.6
55.autosome number	4	O	.	.	1.0	.	1.0
56.Y chromosome size	4	O	X	X	0.6	.	0.6
57.L, frontale 3-spotted?	2	.	.	.	1.0	7	0.8
58.head (other than spots)	3	O	.	.	1.0	7	0.8
59.frontale behind FR,	3	O	.	.	1.0	8	0.7
60.frontale - anteriorly behind FR,	3	U	X	.	0.8	8	0.5
61.parietal eggbursters	4	O	.	.	1.0	8	0.7

Table 3, *cont'd.*

Character	# states	type	my errors	polymor. w/in species	basic weight	dependency groups	altered weight
62.pronotal microtubercles	6	0	.	.	1.0	.	1.0
63.seta FR_1 width	2	.	.	.	1.0	11	0.7
64.seta FR_3 width	2	.	.	.	1.0	11	0.7
65.seta PR_4 length	2	.	.	.	1.0	12	0.6
66.seta PR_{10} length	4	0	X	.	0.8	6,12	0.3
67.gPR & gME lateral setae	2	.	.	.	1.0	6	0.8
68.seta PR_{13} length	2	.	.	.	1.0	12	0.8
69.seta ME_2 length	4	0	X	.	0.8	12	0.5
70.seta ME_{14} length	4	0	.	.	1.0	12	0.6
71.seta TE_8 length	3	0	X	.	0.8	12	0.5
72.seta TE_{11} length	3	0	.	.	1.0	12	0.6
73.seta TE_{11} shape	2	.	.	.	1.0	.	1.0
74.seta TEα (near TE_9)	2	.	.	.	1.0	.	1.0
75.seta EP_1 length	2	.	.	.	1.0	12	0.6
76.segment VIII seta EP_1 width	2	.	.	.	1.0	11	0.7
77.seta ST_2 on segment IX	2	.	.	.	1.0	.	1.0
78.mandible mesal margin	3	0	X	.	0.8	.	0.8
79.L_2 extra setae near FR_3	2	.	X	.	0.8	.	0.8
80.L_2 stipites	2	.	.	.	1.0	.	1.0
81.# long urogomphus setae	3	0	.	.	1.0	.	1.0

5.2 The Phylogenetic Context of *Chrysobracteon*

5.2.1 Suprageneric relationships within the supertribe Trechitae

While relationships of major lineages of Trechitae are not crucial for my study of *Chrysobracteon*, they serve as a useful background within which to ponder the evolution of *Chrysobracteon* and its near relatives. Therefore, I review a few aspects of trechites, concentrating on the tribe Bembidiini.

Four tribes are included within the supertribe: Trechini, Zolini, Pogonini, and Bembidiini (Kryzhanovskij 1976, Erwin 1985). Virtually no cladistic studies on the higher-level relationships of the members of these tribes have been published. Erwin's (1972, 1982) papers are the only available works, and these only deal with a very few aspects of bembidiine phylogeny. A number of non-Hennigian studies include Jeannel (1941), Barr (1971), Schuler (1971), and Perrault (1981); but the character analysis in these is somewhat vague or not explicit. A complete analysis of major evolutionary patterns within trechites is far beyond the scope of the present work.

Fig. 276 presents some names of major groups of trechites, and hypotheses of some possible aspects of their phylogeny; it is based mainly on the previously cited works. The meager cladistic structure illustrated in the figure is in doubt: the monophyly of the groups shown, and their relationships, have not been adequately demonstrated.

Monophyly of Bembidiini

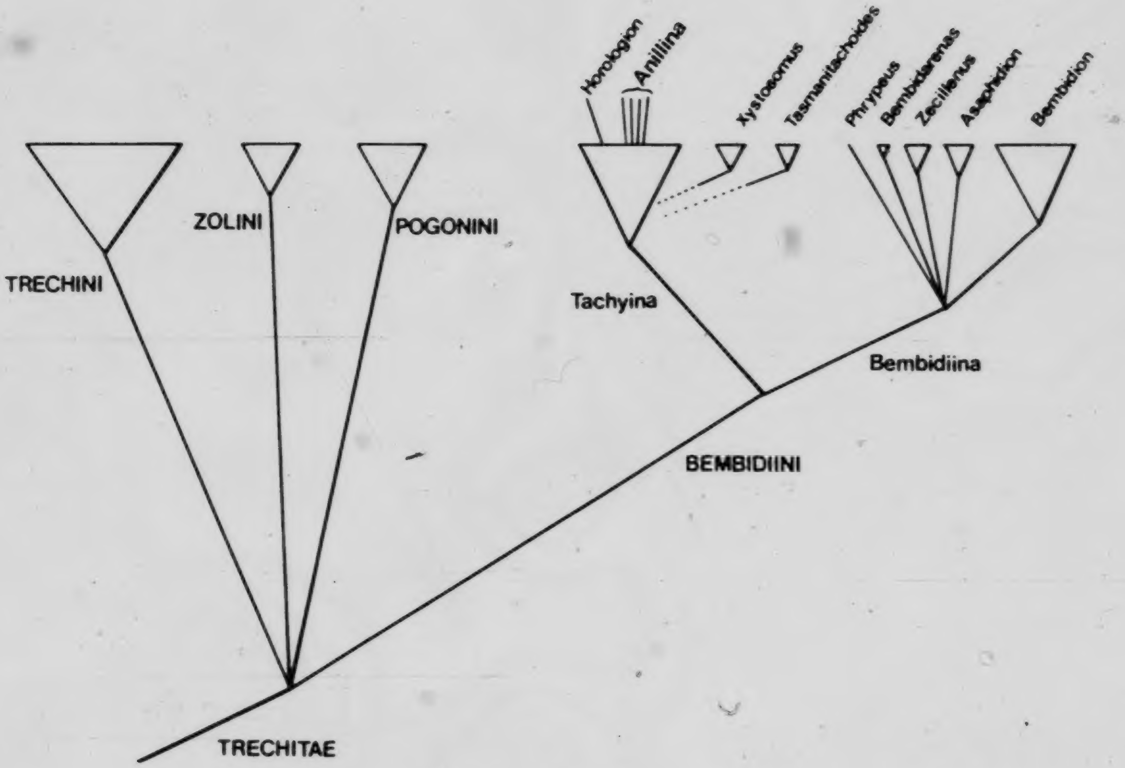
The tribe Bembidiini includes thousands of species of carabids with small or minute adults, which occur throughout the world. The only known derived character linking members of the Bembidiini are the subconical, narrow, and short apical palpomeres (Erwin 1982). However, some trechines (for example, *Oxytrechus* Jeannel and *Perileptus* Schaum) also have relatively small terminal palpomeres. A bembidiine-like palpus occurs as well in the aberrant genus *Gehringia* Darlington, a genus with doubtful affinities to bembidiines. There is some uncertainty about the nature of palpomere evolution, and thus about bembidiine monophyly; the character needs to be studied in more detail.

Generic relationships within Bembidiini

Members of the tribe containing *Bembidion* are organized by some workers into the three subtribes Anillina, Tachyina, and Bembidiina. All are worldwide groups, with the small tachyines being predominantly tropical, the larger bembidiines mainly temperate, and the minute, soil-dwelling anillines occurring in unglaciated regions.

Erwin (1982) proposes that Anillina is a polyphyletic grade derived from the tachyine *Paratachys* Casey and its allies. *Limnastis* and relatives, plus *Horologion* Valentine are also presumably derived from this same group (Barr 1971, Erwin 1982).

Figure 276. Proposed cladistic structure of Trechitae and genera of Bembidiina. Based mainly on Kryzhanovskij (1976) and Erwin (1972, 1982, and 1985).


Horologion
Anillina
Xystosomus
Tasmanitachoides
Phrypeus
Bembidarenas
Zecillenus
Asaphidion
Bembidion
TRECHINI
ZOLINI
POGONINI
Tachyina
Bembidiina
BEMBIDIINI
TRECHITAE

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Among Bembidiina, Erwin (1972) considers *Asaphidion* and *Bembidion* to be sister groups, indicated by common possession of the (presumably derived) brush on male internal sacs. This character state is not found in other Bembidiina, but it is found as well in the tachyine *Xystosomus* Schaum (Erwin 1973), and, perhaps for this reason Erwin (pers. comm. 1983) has suggested that *Xystosomus* is actually a member of Bembidiina, and not a tachyine. Another genus of doubtful affinities is the Australian *Tasmanitachoides* Erwin, now placed in the Tachyina (Erwin 1972). *Phrypeus* is considered by Erwin (1972) to be the sister group of *Asaphidion* + *Bembidion*, with *Bembidarenas* being the sister group of that whole assemblage. Erwin does not treat *Zecillenus*, but in this scheme it would presumably fall outside of the *Asaphidion* + *Bembidion* group because of its supposedly primitive lack of a brush sclerite. Perrault (1981), in contrast, considers the lack of a brush sclerite in *Bembidarenas* and *Phrypeus* (and presumably *Zecillenus*) to be derived, and would include these within *Bembidion* (*sens. lat.*). A more certain sorting of these genera awaits extensive character analysis, including study of promising characters such as male protarsal vestiture, testicular structure, *etc.*.

5.2.2 Monophyly of *Bembidion*

The only character typically cited (Erwin 1972, Lindroth 1980) linking *Bembidion* members is the brush sclerite of the male internal sac (Figs. 99-102, 107). However, *Asaphidion* and *Xystosomus* also possess such a brush, and thus it cannot be considered an autapomorphy of *Bembidion* as the genus now stands. I know of no other possible synapomorphy of members of the genus, and *Bembidion* may be paraphyletic or polyphyletic, with one or more of the less-inclusive genera of Bembidiina derived from within it.

5.2.3 Subgeneric relationships within *Bembidion*

No cladistic analysis of relationships of subgenera of *Bembidion* has been published. Erwin and Kavanaugh (1981) present the only available cladistic analysis of members of the genus, but they deal with relationships within two species groups only.

The main attempt at tracing lineages within the genus was made by Jeannel (1941), with modifications of his scheme proposed by Perrault (1981,1982). These works, however, did not include a cladistic character analysis. Jeannel (1941) lists seven phylogenetic series within the French bembidiine fauna: *Ocys*, *Cillenus*, *Notaphus*, *Bembidion*, *Peryphus*, *Odontium*, and *Asaphidion*. Based on the South American fauna, Jeannel (1962) later removes *Plataphus* from the *Peryphus* series. He does not discuss the interrelationships of these eight series.

Netolitzky (1942), in contrast, distinguished two major phyletic series in his studies of *Bembidion*, the *Notaphus* series (with "free" ed3 and ed5), and the *Peryphus* series (with ed3 and ed5 attached to interneur). He presents a number of other series of evolving lines (based on changes in form of mentum tooth, humeral margin, etc.) interwoven with these two series; but the discussion is lacking clear hypotheses of relationships of taxa.

Perrault (1982) also views *Bembidion* as comprising two major lineages, but of different compositions than Netolitzky's. According to Perrault, *Bembidion* originated in the tropics, with an ancient separation of two stocks leading to the eastern Southern Hemisphere forms on one hand, and to the speciose Northern Hemisphere and South American taxa.

In my opinion, none of these views have been corroborated, and at present must be considered very tentative working hypotheses.

The relationships of the subgenera of *Bembidion* are of importance herein primarily as outgroup cladistic structure is valuable for the outgroup analysis part of my *Chrysobracteon* mental analysis. I am thus most interested in the interrelationships of *Bembidion* species for which I have knowledge about those character systems studied within *Chrysobracteon* (that is, those species for which I have data on most adult, chromosomal, and larval characters). Names of these outgroup species are listed in Tables 4 and 5, along with distribution of states of 81 characters. Some of these characters (for example, 9, 26, 30, 31, and 33) have been used in the past to group *Bembidion* into subgenera or species-groups.

5.3 Cladistic structure of the near relatives of *Chrysobracteon*

Fig. 277 presents my initial conclusions about outgroup relationships. Data used to infer the phylogeny shown are given in Tables 2, 4, and 5; I will now briefly outline the mental analysis that resulted in the outgroup phylogeny. I will discuss only those species shown in Fig. 277; some Palearctic members of *Odontium* are not included on this diagram.

I have tentatively included subgenus *Pseudoperyphus* as the sister group of the *Odontium* subgeneric group. This is based mainly on genitalic characters: all males of *Pseudoperyphus* plus the *Odontium* subgeneric group have genitalia of the same basic form, with a large dorsal plate, relatively long flagellum, and right lobe of CSC present; all female spermathecae are shaped more or less as in Figs. 165-179, with a long, annulated cornu. Some other *Bembidion* have similar male genitalia, but without that exact combination of characters; most notably similar among the few species I have examined are one *Liocosmius* species and *B. planatum*. I have not seen other *Bembidion* with spermathecae matching those of *Pseudoperyphus* and the *Odontium* subgeneric group, except *B. concolor* and *B. salebratum*. *Asaphidion alaskanum* also lacks these states, but as the distribution of male and female genitalic

Table 4. Character states in *Asaphidion alaskanum*, *Bembidion* **distantly related to** *Chrysobracteon*, **and** *Pseudoperyphus*. Species abbreviations: **Asa**: *Asaphidion alaskanum* Wickham, **qua**: *B. quadrimaculatum* (Linné) (from Alberta), **tim**: *B. timidum* LeConte, **gra**: *B. graphicum* Casey, **umb**: *B. umbratum* LeConte, **sco**: *B. scopulinum* Kirby, **obs**: *B. obscurellum* Motschulsky, **pet**: *B. petrosum* Gebler, **cnc**: *B. concolor* Kirby, **sal**: *B. salebratum* LeConte, **pln**: *B. planatum* LeConte, **kup**: *B. "kuprianovi-#1"* (this is the larger and darker of the two species presently included within *B. kuprianovi*), **obt**: *B. obtusum* Serville, **inv**: *B. interventor* Lindroth, **ruf**: *B. rufotinctum* Hayward, **int**: *B. integrum* Casey, **hon**: *B. honestum* Say, **ant**: *B. antiquum* Dejean, **s17**: *B. "sp.17"*, **cha**: *B. chalceum* Dejean. Other symbols, including those for character states, as in Table 2.

Character	**Asa**	**qua**	**tim**	**gra**	**umb**	**sco**	**obs**	**pet**	**cnc**	**sal**	**pln**	**kup**	**obt**	**inv**	**ruf**	**int**	**hon**	**ant**	**s17**	**cha**
Adult external characters																				
NUMBER OF SPECIMENS	*6*	*6*	*6*	*6*	*6*	*6*	*6*	*6*	*6*	*6*	*6*	*5*	*6*	*6*	*6*	*6*	*6*	*6*	*6*	*6*
1. mirrors on interval 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2. mirrors on intervals 4 or 5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3. mirrors on intervals 6 or 7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4. interval 7 mirror isolated?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5. silver spot on interval 4?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6. elytral sculpticell shape	T	-	I	T	I	T	T,I	T	T	T	I	T	T	T	I	T	I	T,I	T	T
7. suborbital setae	2	1	0,1	0,1	0	0	0	0	1	0	1,2	2	0	0,1	1	0	2	2	1	1,2
8. midlateral pronotal setae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
9. ed3 and ed5 - position relative to 3rd interneur	-	A,F	F	F	F	A	A	A	A	A	A	A	A	F,A	A	A	A	A	A	A
10. ed3 and ed5 - position relative to silver spot	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11. # setae between eo4 & eO5	0	0	0	0	0	0	0	0	.13	0	.25	0	0	.14	.14	.14	0	.15	.17	.08
12. # setae ed7 area	1.1	1	1	1	1	1	1	1.1	1	1	1	1	1	1	1	1	1	1	1	1
13. male adhesive setae	.	.	.	.	.	.	.	.	.	.	W	.	.	.	.	.	.	.	.	.
14. protarsomere 4 ventroapical setae	C*	C*	C	F	.	F	.	F	F	.	F	F	.	C*	F	F	F	F	F	F
15. protarsomere 4 setal separation	W*	W*	N	N	N	N	N	N	N	N	N	N	.	W*	N	N	N	N	N	N
16. mandible shape	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
17. lacinia shape	C	.	.	C	.	.	.	C	.	.	C	C	.	C	C	C	C	C	C	C
18. lacinia width	N	.	.	.	.	.	N	N	.	.	N	N	N	W	N	N	N	N	N	N
19. mentum tooth shape	T	T	T	T	R	T	T	T	T	T	T	T	T	T	T	T	T	T	T	T
20. mentum tooth emarginate?	N	N	N	N	N	N	N	N	N	N	N	N	N	Y	N	N	N	N	N	N
21. mentum tooth bulbous?	N	N	N	N	Y	N	N	N	N/Y	N/Y	N	N	N	N	N	N	N	N	N	N
22. mentum epilobes	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
23. pronotal shape	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R
24. pronotal carina	0	3	3	2	2	0,1	2	2	2	0,1	2	2	1,2	1,2	0	0	0	0	0	0
25. metasternum	U	B	B	B	B	B	B	B	B	B	B	B	.	U	U	U	U	U	U	U
26. elytral basal impression	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O
27. angulate humeral margin	A	A	A	A	A	A	A	A	A	S	A	S	M,L	L	A	A	A	A	A	A
28. interneur 4 shape	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O	O

Table 4, *cont'd*.

Character	Asa	qua	tim	gra	umb	sco	obs	pet	cnc	sal	pln	kup	obt	inv	ruf	int	hon	ant	s17	cha
29. elytra around ed3 and ed5 foveolate?	-	N	N	N	N	N	N	N	N	N	N	N/Y	N	N	N	N	N	N	N	N
30. elytral punctures	-	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
31. interneur 8 depth	-	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D
32. interval 5 posteriorly	F	F	F	F	F	F	F	F	F	R	R	R	R	F	F	F	F	F	F	F
33. subapical elytral plica	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
34. male protarsomere 3 shape	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35. protarsomere 4 projection	A	A	S	S	S	.	.	L	.	.	S	..	.	A	.	S	S	S	.	S
Male genitalia																				
NUMBER OF SPECIMENS	*2*	*2*	*2*	*1*	*1*	*2*	*2*	*1*	*2*	*2*	*2*	*2*	*2*	*1*	*3*	*2*	*3*	*4*	*4*	*4*
36. flagellar sheath	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0*	0*	0*
37. CSC right lobe	.	N	N	A	A	N	N	N	N	N	N	A	N	A	W	W	W	W	W	W
38. CSC right lobe ridge	-	0	0	-	-	0	0	0	0	0	0	-	0	-	0	0	0	0	0	0
39. VSP dorsal ridge	-	-	-	-	-	-	0	0	0	0	0	0	0	-	0	0	0	0	0	0
40. VSP dorsal ridge sculpture	-	-	-	-	-	-	0	.	1	1	1	1	.	-	0	0	0	0	1	0
41. dark spot on flagellar sheath	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
42. ostial microtrichial patch size	A	A	A	A	A	L	M/L	M	M	M/L	L	L	S	M	M/L	L	L	L	M/L	L
43. ostial microtrichia	-	-	-	-	-	2	0	2	0	0	0	2	0	2	1	2	2	1,2	0	0
44. ostial sclerotized strip	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
45. pillow with scales	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
46. leftmost central membrane of internal sac	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	L	L	L
47. ventral bulge	0	0	0	0	0	0	0	0	0	0	0	0	0,1	1	0	0	2	1	1	1
48. aedeagal apex	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S	S
Female genitalia																				
NUMBER OF SPECIMENS	*2*	*2*	*2*	*1*	*2*	*2*	*1*	*3*	*2*	*2*	*2*	*2*	*1*	*2*	*1*	*2*	*1*	*2*	*1*	*3*
49. vaginal sclerotized plate	1	1	0	1	1	0	0	0,1	1	1	1	1	1	1	0	0	0	0	0	0
50. spermatheca apically indented?	Y	N	N	N	N	N	Y	Y	N	N	N	N	Y	N	N	N	N	N	N	N
51. stylomere 1 setal length	A	M	A	M	M	M	M	M,A	L	M	A	M	A	A	L	L	L	L	L	L
52. stylomere 2 length	170	130	95	140	125	125	160	150	140	125	250	170	110	165	170	190	170	220	190	160
53. #dorsolateral sensilla	2-3	2-3	2	2	2	1-3	1-2	1-2	2-3	2	0	2-3	2	2	2-3	2-3	1-2	2-3	3-4	2
54. sternum X setation	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L	L
Chromosomes																				
NUMBER OF SPECIMENS	*10*	*4*	*3*	*5*	*4*	*3*	*2*	*7*	*2*	*2*	*7*	*2*	*4*	*7*	*8*	*4*	*3*	*12*	*8*	*11*
55. autosome number	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	22	32	24
56. Y chromosome size	S	.	.	S	S	.	.	A	M,L	M,L	S	S	S	.	.	M	M	M	S	M/L

Table 4, *cont'd.*

Character	Asa	qua	tim	gra	umb	sco	obs	pet	cnc	sal	pln	kup	obt	inv	ruf	int	hon	ant	s17	cha
First instar larva																				
NUMBER OF SPECIMENS	*1*	*2*	*1*	*3*	*2*	*1*	*1*	*3*	*3*	*5*	*1*	*1*	*2*	*5*	.	*1*	.	*1*	.	*4*
57.frontale 3-spotted?	N	N	N	N	N	N	N	N	N	N	N	N	N	N	.	N	.	N	.	N
58.head (other than spots)	L	L	L	L	L	L	L	L	L	L	L	L	L	L	.	L	.	L	.	L
59.frontale behind FR_3	1	0/1	1	1	1	0/1	0	0/1	1	1	0/1	0/1	0/1	1	.	1	.	0	.	1
60.frontale - anteriorly behind FR_3	S	-	M	M	M	S	-	S	S	S/M	S	S	S	S	.	M	.	A	.	M
61.parietal eggbursters	ST	D	D	D	D	D	D	D	D	D	ST	D	D	DST	.	D	.	D	.	D
62.pronotal microtubercles	5	0	0	0	0	0	0	0	0	0	0	0	0	0	.	0	.	0	.	0
63.seta FR_1 width	W	N	N	N	N	N	N	N	N	N	W	N	N	N	.	N	.	N	.	N
64.seta FR_3 length	W	N	N	N	N	N	N	N	N	N	W	N	N	N	.	N	.	N	.	N
65.seta PR_4 size	VS	L	L	L	L	L	L	L	L	L	L	L	L	L	.	L	.	L	.	L
66.seta PR_{10} length	A	L	L	L	L	L	L	L	L	L	L	L	L	L	.	M	.	M	.	L
67.gPR & gME lateral setae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	.	0	.	0	.	0
68.seta PR_{13} length	-	L	L	L	L	L	L	L	L	L	L	L	L	L	.	L	.	L	.	L
69.seta ME_2 length	L	L	L	L	L	L	L	L	L	L	L	L	L	L	.	L	.	M	.	L
70.seta ME_{14} length	-	L	L	L	L	L	L	L	L	L	L	L	L	L	.	L	.	L	.	L
71.seta TE_6 length	S	L	L	L	L	L	L	L	L	L	L	L	L	L	.	L	.	L	.	L
72.seta TE_{11} length	-	L	L	L	L	L	L	L	L	L	L	L	L	L	.	L	.	L	.	L
73.seta TE_{11} shape	-	W	W	W	W	W	W	W	W	W	W	W	W	W	.	W	.	W	.	W
74.seta $TE\alpha$ (near TE_6)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	.	0	.	0	.	0
75.seta EP_1 length	S	L	L	L	L	L	L	L	L	L	L	L	L	L	.	L	.	L	.	L
76.segment VIII seta EP_1 width	-	W	W	N	N	W	W	W	W	W	W	W	W	N	.	N	.	.	.	W
77.seta ST_2 on segment IX	0	0	0	0	0	0	0	0	1	1	0	0	0	0	.	0	.	.	.	0
78.mandible mesal margin	0	0/1	1/0	1	1	1/2	1	0,1	1	1,0	1	2	1	0	.	1	.	2	.	2
Second instar larva																				
NUMBER OF SPECIMENS	.	.	.	*1*	*1*	.	*1*	*1*	*1*	*1*	.	.	.	*1*	.	.	.	.	.	.
79.extra setae near FR_3	.	.	.	0	0	.	0	0	0	0	.	.	.	0	.	.	.	.	.	.
80.L_2 stipites	.	.	.	4	4	.	3	3	3	3	.	.	.	3	.	.	.	.	.	.
81.# long urogomphus setae	.	.	.	7	7	.	7	7	7	7	.	.	.	7	.	.	.	.	.	.

Table 5. Character states in *Ochthedromus* and *Odontium*.

Species abbreviations: **ame**: *B. americanum* Dejean, **bif**: *B. bifossulatum* LeConte, **che**: *B. cheyennense* Casey, **chp**: *B. chloropus* Bates, **fus**: *B. fusiforme* Netolitzky, **aep**: *B. aeneipes* Bates, **nra**: *B.* sp. nr. *aenulum*, **aen**: *B. aenulum* Hayward, **dur**: *B. durangoense* Bates, **arz**: *B. arizonae* Lindroth, **cnf**: *B. confusum* Hayward, **scu**: *B. sculpturatum* (Motschulsky), **crt**: *B. carinatum* (LeConte), **cox**: *B. coxendix* Say, **rob**: *B. robusticolle* Hayward, **prs**: *B. persimile* Morawitz, **str**: *B. striatum* (Fabricius), **for**: *B. foraminosum* Sturm, **bow**: *B. bowditchii* LeConte.

Other symbols, including those for character states, as in Table 2.

	Ochthed.			*Odontium*															
Character	**ame**	**bif**	**che**	**chp**	**fus**	**aep**	**nra**	**aen**	**dur**	**arz**	**cnf**	**scu**	**crt**	**cox**	**rob**	**prs**	**str**	**for**	**bow**
Adult external characters																			
NUMBER OF SPECIMENS	*4*	*6*	*6*	*3*	*3*	*6*	*2*	*6*	*4*	*6*	*6*	*5*	*2*	*6*	*4*	*6*	*6*	*6*	*6*
1. mirrors on interval 3	0	2	2	1	2	2	0	0	0	0	0	0	0	1	0	1	1	1	1
2. mirrors on intervals 4 or 5	0	2	2	1	2	2	0	0	0	0	0	0	0	1	0	1	1	1	1
3. mirrors on intervals 6 or 7	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
4. interval 7 mirror isolated?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5. silver spot on interval 4?	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6. elytral sculpticell shape	I	I/T	I/T	I	I	I	T	I	I	T	T	I/T	I/T	I	I,T	I	I	I	I
7. suborbital setae	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0,1	0,1	2	1	0
8. midlateral pronotal setae	1	1	1	0	0	0	0	0	0	0	1	1	1	1,0	1	1	1	1	1
9. ed3 and ed5 - position relative to 3rd interneur	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A,F	A
10. ed3 and ed5 - position relative to silver spots	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11. # setae between eo4 & eO5	0	0	.14	0	0	.10	0	0	0	0	.08	0	.33	.08	0	.10	.08	.08	.29
12. # setae ed7 area	1	1	1	1	1	1.1	1	1	1	1	1	1	1	.94	1	1	1	1	1.1
13. male adhesive setae	.	W	W	W	W	W	W	W	W	W	W	.	W	W	W	.	W	.	W
14. protarsomere 4 ventroapical setae	.	F	F	.	.	.	F	F	.	F	F	F	F	F	.	F	F	.	F
15. protarsomere 4 setal separation	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
16. mandible shape	C	C	C	C	C	C	C	C	C	S	S	S	C	C	C	C	C	C	C
17. lacinia shape	C	C	C	C	C	C	C	C	C	S	S	S	C	C	C	C	C	C	C
18. lacinia width	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
19. mentum tooth shape	R/T	T	R	T	T	T	T	T	T	T/R	R	R	T	T	T	T	T	T	T
20. mentum tooth emarginate?	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
21. mentum tooth bulbous?	N	N	Y	N	N	N	N	N	N	N	Y	N	N	N	N	N	N	N	N
22. mentum epilobes	1	1	1	1	1	1	1	1	1	1	0	1	1	0/1	1	1	1	1	1
23. pronotal shape	R	R	R	T	T	T	R/T	R	R	R	R	R	R	R	R	R	R	R	R
24. pronotal carina	0	0	0	0	0	0	0	0	1	1	1	2	1	1	3	1	0,1	0	0,1
25. metasternum	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U	U
26. elytral basal impression	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0,1	0,1	0,1
27. angulate humeral margin	M	S,M	S,M	L	L	L	L	L	L	L	L	L	L	L	L	L	M	S,M	M

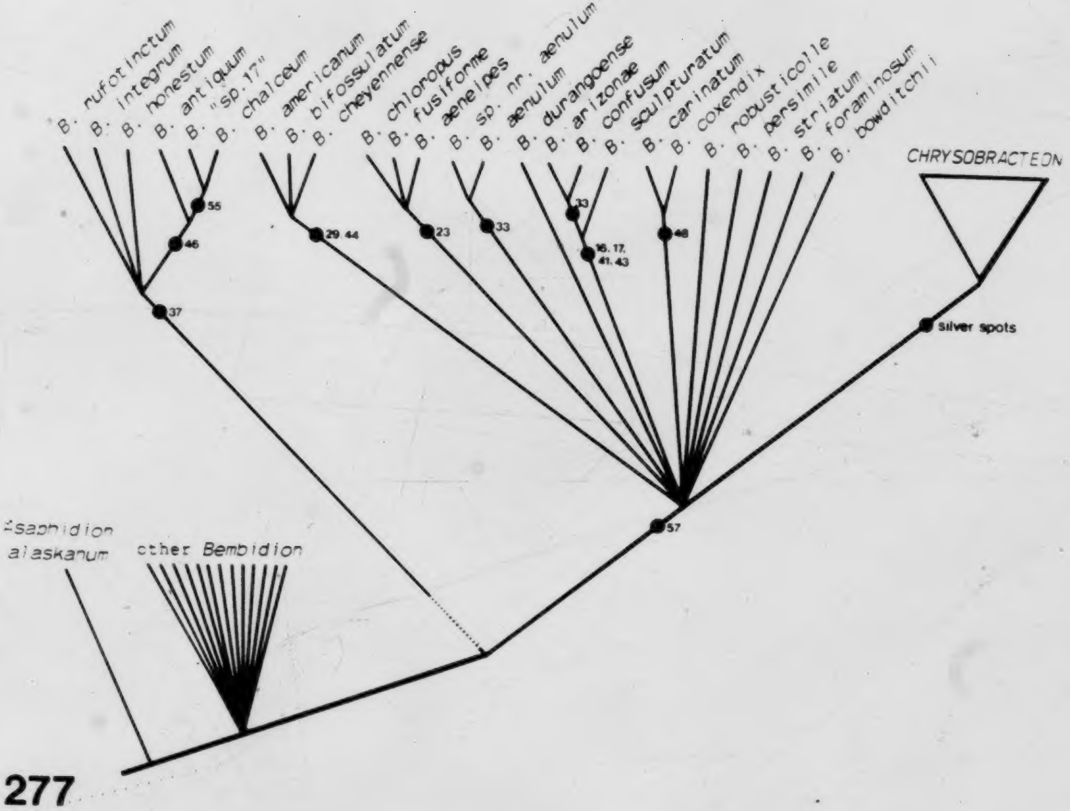
Table 5, *cont'd.*

	Ochthed.			*Odontium*															
Character	**ame**	**bif**	**che**	**chp**	**fus**	**aep**	**nra**	**aen**	**dur**	**arz**	**cnf**	**scu**	**crt**	**cox**	**rob**	**prs**	**str**	**for**	**bow**
28. interneur 4 shape	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29. elytra around ed3 and ed5 foveolate?	Y	Y	Y	N	N	N	N	N	N	N	N	N	N	N	N	N	N	Y	N
30. elytral punctures	C	C	C	C	C	C	C	C	C	T	C/T	T	T	C/T	C	C	C	C	C
31. interneur 8 depth	S/D	S/D	S/D	D	D	D	D	S/D	S	S/D	S/D	S/D	S/D	S/D	S/D	S	S	S	S
32. interval 5 posteriorly	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F
33. subapical elytral plica	2	2	2	2	2	2	0	0	2	1	1	2	2	2	2	2	2	2	2
34. male protarsomere 3 shape	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
35. protarsomere 4 projection	.	L	.	.	.	S	L	L	S	L	L	L	S	S	.	S	S	L	L
Male genitalia																			
NUMBER OF SPECIMENS	*1*	*3*	*3*	*1*	*1*	*2*	*1*	*3*	*1*	*4*	*4*	*1*	*1*	*3*	*1*	*2*	*2*	*2*	*4*
36. flagellar sheath	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37. CSC right lobe	N	N/W	N/W	N	N	N	N	N	N	N	N	N	N	N	N	N	.	N	N
38. CSC right lobe ridge	0	0	0	0	0	0	0	0	2	0	0	0	0	0,2	0	1,2	.	1	0
39. VSP dorsal ridge	0	0	0	0	0	0	0	0	2	0	0	0	1	1	0	0	0	0	0
40. VSP dorsal ridge sculpture	1	1	1	1	0/1	0	0	0/1	1	0	0	.	0	0/1	0	1	1	1	0
41. dark spot on flagellar sheath	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	.	0	0	0
42. ostial microtrichial patch size	L	L	L	M	S	A	M	L	L	L	L	L	L	L	L	L	L	L	L
43. ostial microtrichia	0	0	0	1	0	0	0	1	1	2*	2*	2*	0	0	1/2	1	0	1	0
44. ostial sclerotized strip	1*	1*	1*	0	0	1	0	0	0	0	0	0	0	0	0	0	.	0	1
45. pillow with scales	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
46. internal sac leftmost central membrane	S	S	S	S	S	L	S	S	S	S	S	S	S	S	S	S	S	S	S
47. ventral bulge	0/1	2	1,2	0	0	0	0	0	0	1,0	0	0	0	0	0	1	0	0,1	0
48. aedeagal apex	S	S	S	S	S	S	S	S	S	S	S	S	B	B	S	S	S	S	S
Female genitalia																			
NUMBER OF SPECIMENS	*1*	*1*	*1*	.	.	*1*	.	*3*	*1*	*1*	*3*	.	.	*3*	*1*	*1*	*2*	*1*	*3*
49. vaginal sclerotized plate	0	0	0	.	.	0	.	0	0	0	0	.	.	0	0	0	0	0	0
50. spermatheca apically indented?	N	N	N	.	.	N	.	N	N	N	N	.	.	N	N	N	N	N	N
51. stylomere 1 setal length	M	M	M	.	.	S	.	L	M	L	L	.	.	M	S	M	M	M	M
52. stylomere 2 length	130	200	180	.	.	180	.	110	160	170	190	.	.	195	360	190	190	180	180
53. #dorsolateral sensilla	2	2	2-3	.	.	2	.	4-5	2-3	3	2-3	.	.	1-3	3	2	2-4	2-3	1-2
54. sternum X setation	L	L	L	.	.	L	.	L	L	L	L	.	.	L	L	L	L	L	L
Chromosomes																			
NUMBER OF SPECIMENS	*2*	*5*	*1*	.	.	.	.	*4*	.	*4*	*7*	.	.	*23*	.	.	*2*	.	*7*
55. autosome number	22	22	22	.	.	.	.	22	.	22	22	.	.	22	.	.	22	.	22

Table 5, *cont'd.*

	Ochthed.			*Odontium*															
Character	**ame**	**bif**	**che**	**chp**	**fus**	**aep**	**nra**	**aen**	**dur**	**arz**	**cnf**	**scu**	**crt**	**cox**	**rob**	**prs**	**str**	**for**	**bow**
56. Y chromosome size	.	.	.	.	.	.	.	S	.	S	S	.	.	S	.	.	S	.	S
First instar larva																			
NUMBER OF SPECIMENS	.	.	*3*	.	.	.	.	*1*	.	.	*1*	.	.	*3*	.	.	.	*2*	*7*
57. frontale 3-spotted?	.	.	Y	.	.	.	.	Y/N	.	.	Y	.	.	Y	.	.	.	Y	Y
58. head (other than spots)	.	.	L	.	.	.	.	L	.	.	L	.	.	L	.	.	.	L	L
59. frontale behind FR_3	.	.	1	.	.	.	.	0	.	.	1	.	.	1	.	.	.	1	1
60. frontale - anteriorly behind FR_3	.	.	M	.	.	.	.	A	.	.	M	.	.	M	.	.	.	M	M
61. parietal eggbursters	.	.	D	.	.	.	.	LT*	.	.	D	.	.	D	.	.	.	D	D
62. pronotal microtubercles	.	.	3	.	.	.	.	0	.	.	1	.	.	1	.	.	.	0	0
63. seta FR_1 width	.	.	N	.	.	.	.	N	.	.	N	.	.	N	.	.	.	N	N
64. seta FR_3 length	.	.	N	.	.	.	.	N	.	.	N	.	.	N	.	.	.	N	N
65. seta PR_4 length	.	.	L	.	.	.	.	L	.	.	L	.	.	L	.	.	.	L	L
66. seta PR_{10} length	.	.	S	.	.	.	.	L	.	.	L	.	.	L	.	.	.	L	L
67. gPR & gME lateral setae	.	.	O	.	.	.	.	O	.	.	O	.	.	O	.	.	.	O	O
68. seta PR_{13} length	.	.	L	.	.	.	.	L	.	.	L	.	.	L	.	.	.	L	L
69. seta ME_2 length	.	.	S/M	.	.	.	.	L	.	.	L	.	.	L	.	.	.	L	L
70. seta ME_{14} length	.	.	L	.	.	.	.	L	.	.	L	.	.	L	.	.	.	L	L
71. seta TE_4 length	.	.	S	.	.	.	.	L	.	.	L	.	.	L	.	.	.	L	L
72. seta TE_{11} length	.	.	L	.	.	.	.	L	.	.	L	.	.	L	.	.	.	L	L
73. seta TE_{11} shape	.	.	W	.	.	.	.	W	.	.	W	.	.	W	.	.	.	W	W
74. seta TEα (near TE_9)	.	.	O	.	.	.	.	O	.	.	O	.	.	O	.	.	.	O	O
75. seta EP_1 length	.	.	L	.	.	.	.	L	.	.	L	.	.	L	.	.	.	L	L
76. segment VIII seta EP_1 width	.	.	N	.	.	.	.	N	.	.	N	.	.	N	.	.	.	N	N
77. seta ST_2 on segment IX	.	.	O	.	.	.	.	O	.	.	O	.	.	O	.	.	.	O	O
78. mandible mesal margin	.	.	O	.	.	.	.	O/1	.	.	O/1	.	.	O	.	.	.	O	O
Second instar larva																			
NUMBER OF SPECIMENS	.	.	.	.	.	.	.	*1*	.	.	*1*	.	.	.	.	.	.	*1*	.
79. extra setae near FR_3	.	.	.	.	.	.	.	O	.	.	O	.	.	.	.	.	.	O	.
80. L_2 stipites	.	.	.	.	.	.	.	3	.	.	3	.	.	.	.	.	.	3	.
81. # long urogomphus setae	.	.	.	.	.	.	.	7	.	.	7	.	.	.	.	.	.	7	.

Figure 277. Proposed cladistic structure of near relatives of *Chrysobracteon*. Numbers below a clade are the numbers of characters that support monophyly of the clade (see Tables 2, 4 and 5); derived states that characterize each clade are discussed in the text.


B. rufotinctum
B. integrum
B. honestum
B. antiquum
B. "sp.17"
B. chalceum
B. americanum
B. bifossulatum
B. cheyennense
B. chloropus
B. fusiforme
B. aeneipes
B. sp. nr. aenulum
B. aenulum
B. durangoense
B. arizonae
B. confusum
B. sculpturatum
B. carinatum
B. coxendix
B. robusticolle
B. persimile
B. striatum
B. foraminosum
B. bowditchii
CHRYSOBRACTEON
55
46
37
29 44
23
33
33
16, 17, 41, 43
46
silver spots
57
Asaphidion alaskanum
other Bembidion

277

characters has not been carefully examined throughout most *Bembidion* and other genera, I am not confident that the states in *Pseudoperyphus* and the *Odontium* subgeneric group represent synapomorphies linking the groups. I thus consider these genitalic characters only tentative evidence of relationship of the groups.

The monophyly of *Pseudoperyphus* species is supported by the exceptionally thick, sclerotized ventral margin of the right lobe of the CSC of the male internal sac (character 37); the margin is much thinner in all *Odontium* subgeneric group members, as well as more-distantly related *Bembidion*. Within *Pseudoperyphus*, *B. antiquum*, *B. chalceum*, and *B. "sp.17"* are linked by possession of large scales on the leftmost central membrane of the inverted internal sac (character 46); this state has arisen independently in *B. (Odontium) aeneipes*. I have also tentatively grouped *B. chalceum* and *B. "sp.17"*, based upon the high, derived chromosome number in the two species ($2n=24+XY$ in *B. chalceum* and $2n=32+XY$ in *B. "sp.17"* as opposed to the primitive $2n=22+XY$; character 55).

One subgenus linked to *Pseudoperyphus* by Hatch (1950), is the Holarctic *Hirmoplataphus* Netolitzky. The two members of *Hirmoplataphus* that I studied, *B. concolor* and *B. salebratum*, share a number of traits with members of *Pseudoperyphus* and the *Odontium* subgeneric group. In addition to the similar spermathecae, first instars of both species have seta ST_2 on abdominal segment VIII, a trait shared with some *Chrysobracteon*, and *B. concolor* females have exceptionally long female S1 setae, similar to the states in *Pseudoperyphus* and *B. stenoderum*. The larval setae are probably convergent, and, if it were not for the similar spermathecae, I would presume that the long S1 setae are also convergent between *Hirmoplataphus* and the other *Bembidion*. It is, however, possible that *Hirmoplataphus* is the sister group of *Pseudoperyphus* + the *Odontium* subgeneric group, and long S1 setae are plesiomorphic within the clade. I do not consider the evidence compelling, and leave the two *Hirmoplataphus* within the unresolved mass of "other *Bembidion*" of Fig. 277.

The monophyly of the *Odontium* subgeneric group is established mainly on the basis of the first instar larval coloration: the three-spotted frontale found in all members of the group (except *B. argenteolum*, *B. alaskense*, *B. carinula*, and *B. lapponicum*, all clearly *Chrysobracteon*) is unique among studied *Bembidion* and *Asaphidion* (character 57). Spots are present in *B. balli*, *B. foveum*, and *B. zephyrum*, but do not contrast enough against background color to be seen in Figs. 210, 211, and 217. The lack of spots in the other four *Chrysobracteon* is not too troublesome. Note that the lateral frontal spots are in the region of prominent frontal microsculpture (compare Figs. 194 and 230); this frontal microsculpture presumably serves an egg-bursting function. Dark spots of carabid larval heads, when present, are generally around egg bursters (Yves

Bousquet, pers. comm. 1985). It is thus not surprising, perhaps, that *B. alaskense*, *B. carinula*, and *B. lapponicum* all lack spotted frontales: these are the species in which egg-bursting function has apparently shifted to the prominent parietal denticles, and whose frontales have sparse or no microsculpture (compare frontal microsculpture of *B. alaskense*, *B. carinula*, and *B. lapponicum* (Figs. 227-229) with that of *B. foveum*, *B. punctatostriatum*, and *B. levettei levettei* (Figs. 226, 230, 231)). (This does not, however, explain why *B. alaskense*, *B. carinula*, and *B. lapponicum* also lack dark spots around the parietal egg bursters.) The lack of frontal spots is thus probably secondary, derived within *Chrysobracteon* in concert with the development of exceptionally large parietal egg bursters.

Within the *Odontium* subgeneric group, several clades are apparent. Evidence for the monophyly of each will be discussed in turn.

Ochthedromus. Members of *Ochthedromus* share several derived features, including: foveae around elytral setae ed3 and ed5 (character 29); exceptionally long and numerous mental and submental setae; an ostial sclerotized strip in the male internal sac of a rather beaded appearance (character 44). The latter two states are unique within *Bembidion* I have seen. Relationships of the three included species are unclear.

B. aeneipes + *B. fusiforme* + *B. chloropus*. Members share fusiform shape, with the straight-sided, broadly based pronotum with prominent front angles (character 23).

B. aenulum and *B.* sp. nr. *aenulum* are linked by a common lack of a subapical plica on the elytron (Fig. 65; character 33). All other bembidiines I have seen possess a plica.

B. sculpturatum + *B. confusum* + *B. arizonae*. The members of this distinctive clade share a dark, sclerotized strip on the flagellar sheath just ventral to the dorsal plate in inverted internal sacs (character 41); an ostial microtrichial patch with sparse, multitoothed combs with small teeth (character 43); straight, thin laciniae with short apical setae (Fig. 42; character 17); abruptly narrowed and apically straight mandibles (Fig. 28; character 16). *B. confusum* is united with *B. arizonae* by common possession on elytra of a subapical plica that is not confluent with the side margin (Fig. 66; character 33), a trait unique among the bembidiines I have studied.

The only other clade I recognized within the *Odontium* subgeneric group, other than in *Chrysobracteon*, was that composed of *B. carinatum* + *B. coxendix*, supported by presence of an abruptly ventrally bent aedeagal apex (character 48).

5.4 Monophyly of *Chrysobracteon*

The only known autapomorphy of *Chrysobracteon* is the presence of elytral silver spots around ed3 and ed5. This state is, to my knowledge, unique within the Trechitae. Some near-outgroup species also have the elytral surface around ed3 and ed5 modified, but in different ways from *Chrysobracteon*. For example, *Ochthedromus* and *B. (Odontium) foraminosum* specimens have the region around ed3 and ed5 foveolate. In *B. foraminosum* the microsculpture is distinctly modified around the setae, with the sculpticells stretched. However, no distinct, granulate silver spots are present in either group. I conclude, therefore, that *Chrysobracteon* is monophyletic, although the evidence is not overwhelming.

5.5 Phylogeny of *Chrysobracteon*

5.5.1 Mental analysis

To begin the analysis, I chose as ancestral to *Chrysobracteon* a state that allows for a simple hypothesis of outgroup evolution. I made such a choice using the outgroup algorithm of Maddison *et al.* (1984).

However, the outgroup relationships are uncertain for *Chrysobracteon* (Fig. 277), and so the algorithm could not be applied directly. This uncertainty in outgroup structure reflects a number of possible resolutions of relationships. In fact, for this study the number of possible full resolutions of near-outgroup (*Pseudoperyphus* + *Odontium* subgeneric-group) structure shown in Fig. 277 is 1.9 trillion (see Felsenstein 1978). The outgroup algorithm could be applied to each possible resolution, and for each a set of possible ancestral state assessments could be obtained; but this would be dreadfully time-consuming. Fortunately, for some characters the outgroup uncertainties are irrelevant for the outgroup analysis, and an unequivocal ancestral state assessment is produced; this occurs when all possible resolutions yield the same most parsimonious hypothesis of ancestral state (for example, if the character is invariant among the outgroups). But for most characters, different outgroup resolutions will yield different assessments of ancestral state. For these characters, I mentally juggled the outgroups in my head to come up with as many assignments of ancestral states. An example is warranted.

Consider character 1. If *B. americanum* is the sister group of *B. bifossulatum*, and *Ochthedromus* the sister group of *Chrysobracteon*, with (*B. chloropus* + *B. fusiforme*) + *B. aeneipes* the next-most distant sister group, then the ancestral state assessment for *Chrysobracteon* is state 2 (slight mirrors present). If, however, *B. durangoense* is the sister group of *Chrysobracteon*, with *B. robusticolle* next down the line, then state 0 is the assessment. Another arrangement of outgroups would yield state 1; no arrangements would yield state 3. Thus the full range of possible ancestral state assessments is 0-2 (Table 6, character 1, rightmost column).

Other characters were treated similarly. For each, I condensed outgroup information, recording the range of preferred ancestral states (Table 6). Taking these into account will at least partly allow for simple hypotheses of outgroup evolution. It is not an ideal technique, as character interactions are not taken into account (Maddison *et al.* 1984).

Table 6. Hypothesized ancestral states of various *Chrysobracteon* **ancestors and relatives.** Information condensed from Tables 4 and 5 using the outgroup algorithm of Maddison *et al.* (1984), as explained in text.

og states: list of states found in the outgroup species of Tables 4 and 5.

For rightmost four columns, the entries are the full range of ancestral state assessments, under the different possible outgroup resolutions, for the following nodes: **Pseud+Odon-g**: outgroup node (Maddison *et al.* 1984) of *Pseudoperyphus*+*Odontium* subgeneric-group; **Pseudo**: outgroup node of *Pseudoperyphus*; **Odont-subg-g**: outgroup node of *Odontium* subgeneric-group; **Chryso**: outgroup node of *Chrysobracteon*.

Parentheses enclose one possible equivocal ancestral state assessment. For example, for character 16, one resolution would yield for *Chrysobracteon* "C", and another "C or S". For character 28 one possible outgroup resolution will yield an assessment for *Chrysobracteon* of "N", another of "Y". Characters with only one entry have the same assessment under all possible outgroup resolutions.

Character	og states	Pseud+Odon-g	Pseudo	Odont-subg-g	Chryso
1. mirrors on interval 3	O,1,2	O	O	O	O-2
2. mirrors on intervals 4 or 5	O,1,2	O	O	O	O-2
3. mirrors on intervals 6 or 7	O,1	O	O	O	O-1
4. interval 7 mirror isolated?	-	-	-	-	-
5. silver spot on interval 4?	-	-	-	-	-
6. elytral sculpticell shape	I,I/T,T	I,T	I,T	I,T	I-(I/T,T)
7. suborbital setae	O,1,2	O-2	(O,1)-(1,2)	O-2	O-2
8. midlateral pronotal setae	O,1	1	1	1	O,1
9. ed3 and ed5 - position relative to interneur 3	A,F	A,F	A	A,(A,F)	A
10. ed3 and ed5 - position relative to silver spot	-	-	-	-	-
11. # setae between eo4 & eO5	O-.33	O,(.13-.25)	(O-.14) - (.14-.15)	O,(.14-.15)	O, (.10-.29), (.14-.15)
12. # setae ed7 area	.94-1.1	1-1.1	1	1,(1-1.1)	1,(1-1.1)
13. male adhesive setae	W	W		W	W
14. protarsomere 4 ventroapical setae	F,C	F,C	F	F,(F,C)	F
15. protarsomere 4 setal separation	N,W	N,W	N	N,(N,W)	N
16. mandible shape	C,S	C	C	C	C,(C,S)
17. lacinia shape	C,S	C	C	C	C,(C,S)
18. lacinia width	W,N	(W,N),N	N	N	N
19. mentum tooth shape	R,T	(R,T),T	T	T	T,(R/T,R)
20. mentum tooth emarginate?	Y,N	(Y,N),N	N	N	N
21. mentum tooth bulbous?	Y,N	N,(Y,Y/N)	N	N,(N,N/Y)	N
22. mentum epilobes	O,1	(O,1),1	1	1	1
23. pronotal shape	R,R/T,T	R	R	R	R,(R-T)
24. pronotal carina	O,1,2,3	(O,1)-3	O	O,(O-3)	O,(1-3)
25. metasternum	U,B	U,B	U	U,(U,B)	U
26. elytral basal impression	O,1,2	O	O	O	O,(1-2)
27. angulate humeral margin	A,S,M,L	A-L	A	A	(A-M),L

Table 6, *cont'd.*

Character	og states	Pseud+Odon-g	Pseudo	Odont-subg-g	Chryso
28. interneur 4 shape	O	O	O	O	O
29. elytra around ed3 and ed5 foveolate?	N,Y	N,(N,N/Y)	N	N	N,Y
30. elytral punctures	C,C/T,T	C	C	C	C,(C/T-T)
31. interneur 8 depth	S,S/D,S	D	D	D	S-D
32. interval 5 posteriorly	F,R	F,R	F	F(F,R)	F
33. subapical elytral plica	O,1,2	2	2	2	(O-2),2
34. male protarsomere 3 shape	O	O	O	O	O
35. protarsomere 4 projection	A,S,L	A,(S,L)	S	(A,S),S	S,L
36. flagellar sheath	O,O*	O	O,(O,O*)	O	O
37. CSC right lobe	A,N,W	A,N	W	(A,N),(A,W)	N,N/W
38. CSC right lobe ridge	O,1,2	O	O	O	O,(1,2)
39. VSP dorsal ridge	O,1,2	O	O	O	O,(1,2)
40. VSP dorsal ridge sculpture	O,1	(O,1),1	O	O,(O,1)	O,1
41. dark spot on flagellar sheath	O,1	O	O	O	O,(O,1)
42. ostial microtrichial patch size	A,S,M,L	A-L	(M/L,L),L	(A-M/L),L	(S-M/L),L
43. ostial microtrichia	O,1,2	O-2	1,2	(O,1),2	O-2
44. ostial sclerotized strip	O,1,1*	O,(O,1)	O	O	O,(1,1*)
45. pillow with scales	O	O	O	O	O
46. internal sac leftmost central membrane	S,L	S	S,(S,L)	S	S
47. ventral bulge	O,1,2	O,(O,1)	O,(1,2)	O,1	O,1
48. aedeagal apex	S,B	S	S	S	S,(S,B)
49. vaginal sclerotized plate	O,1	O,1	O	O,(O,1)	O
50. spermatheca apically indented?	N,Y	N,Y	N	N,(N,Y)	N
51. stylomere 1 setal length	A,S,M,L	A-(M,L)	L	(A-L),L	S-L
52. stylomere 2 length	95-360	(95-110), (170-250)	170-190	(110-170),190	(110-160), (195-360)
53. #dorsolateral sensilla	O-5	(O,1)-(2-3)	2,(2-3)	2,(2-3)	2,(3-4)
54. sternum X setation	L	L	L	L	L
55. autosome number	22,24,32	22	22	22	22
56. Y chromosome size	S,M,L	S,(M,L)	M	(S,M),M	S,(S,M)
57. frontale 3-spotted?	N,Y	N	N	N	(N-N/Y),Y
58. head (other than spots)	L	L	L	L	L
59. frontale behind FR_1	O,1	(O-O/1),1	1	(O/1,1),1	(O/1,1),1
60. frontale - anteriorly behind FR_1	A,S,M	S-M	M	(S-M),M	M
61. parietal eggbursters	D,ST,LT*	D,ST	D	D,(D,ST)	D,(D-ST)
62. pronotal microtubercles	O,1,3,5	O,(O-5)	O	O	O,(1-3)
63. seta FR_1 width	N,W	N,W	N	N,(N,W)	N

Table 6, *cont'd.*

Character	og states	Pseud+Odon-g	Pseudo	Odont-subg-g	Chryso
64. seta FR_3 width	N,W	N,W	N	N,(N,W)	N
65. seta PR_4 length	VS,L	(VS-L),L	L	L	L
66. seta PR_{10} length	A,S,M,L	(A-L),L	M	M,(M,L)	M,L
67. gPR & gME lateral setae	O,1	O,(O,1)	O	O	O
68. seta PR_{13} size	L	L	L	L	L
69. seta ME_2 length	L	L	L	L	L
70. seta ME_{14} length	L	L	L	L	L
71. seta TE_6 length	S,L	(S,L),L	L	L	L
72. seta TE_{11} length	L	L	L	L	L
73. seta TE_{11} shape	W	W	W	W	W
74. seta TEα (near TE_8)	O	O	O	O	O
75. seta EP_1 length	S,L	(S,L),L	L	L	L
76. segment VIII seta EP_1 width	N,W	N,W	(N,W)	N,W	N
77. seta ST_2 on segment IX	O,1	O,1	O	O,(O,1)	O
78. mandible mesal margin	O,1,2	O-(1/2,2)	(1,2)	(O,1),(1/2,2)	O,(O/1)
79. extra setae near FR_3	O	O	.	O	O
80. L_2 stipites	3,4	3,4	.	3,4	3,(3,4)
81. # long urogomphus setae	7	7	.	7	7

The next step in the analysis is the deciphering of lineages within *Chrysobracteon*. Not all 81 characters are useful for this. Fourteen of the characters are invariant within *Chrysobracteon* (9, 16, 17, 23, 28, 31-33, 37, 41, 48-50, 80); these include some of the characters that were used to infer outgroup relationships shown in Fig. 277. As well, outgroup analysis indicated that in 21 of the 67 remaining characters, the outgroup information at hand provided no initial clue as to ancestral states of *Chrysobracteon*.

The assessments of ancestral states for the remaining 46 characters lead to hypotheses of derived states within *Chrysobracteon* plus its stem group. The distributions of these derived states are shown in Table 7. Seventeen of these characters (12, 15, 18, 45, 47, 52, 54, 61, 62, 65, 67, 68, 70, 72-75) showed only states autapomorphic for single species, and thus they provide no evidence yet for joining species together. Thus, the remaining 29 characters are the basis for the next step of the analysis.

Table 7. Character states derived within *Chrysobracteon* **+ its stem group.**

Species abbreviations: **bl**: *B. balli*, **fo**: *B. foveum*, **ar**: *B. argenteolum*, **al**: *B. alaskense*, **sm**: *B. semenovi*, **st**: *B. stenoderum*, **ca**: *B. carinula*, **vx**: *B. velox*, **lp**: *B. lapponicum*, **pn**: *B. punctatostriatum*, **hs**: *B. hesperium*, **lq**: *B. lorquinii*, **ze**: *B. zephyrum*, **lvl**: *B. levettei levettei*, **lvc**: *B. levettei carrianum*, **in**: *B. inaequale*, **lt**: *B. litorale*, **bk**: *B. baikaloussuricum*.

'.': plesiomorphic states; '1', '2', '3': derived states of the transformation series, in order; '0', '-1': derived states of the tranformation series, leading from the plesiomorphic state in the reverse direction from the 1, 2, 3 transformation series. Other symbols as in Table 2.

The continuous character 11 was divided into three derived states: '1' (values .40-.80), '2' (values 1.8-2.1), '3' (value of 4).

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	bk
1. mirrors interval 3	.	.	1	1	.	1	1	1	1	1	.,1	1	1	1	1	1	1	1
2. mirrors on intervals 4 or 5	.	.	.,1	.,1	.	1	.	.	.,1	.	1	1	1	1	1	1	1	1
3. mirrors on intervals 6 or 7	.	.	.	.	.	1,.	.	.	.,1	.	1,.	.	1,2	2	2	2	2	2
11. # setae between eo4 & e05	.	1	2	.	3	.	1	.	.	2	.	.	.	.	.	.	.	.
12. # setae ed7 area	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
13. male adhesive setae	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
14. protarsomere 4 ventoapical setae	.	.	1	1	1	.	.	.	.	1	.	.	.	.	.	.	.	.
15. protarsomere 4 setal separation	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
18. lacinia width	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
20. mentum tooth emarginate?	.	.	.,1	.,1	1	.	.	.	.	.	1,.	1	.,1	.	.	.	1	.,1
21. mentum tooth bulbous?	.	.	.	.	.	.	.	.	.	1	.	.	.	1	1	1	.	./1
22. mentum epilobes	.	.	.	.	.	.	.	.	.	1	.	.	.	1	1	1	.	.
28. interneur 4 shape	.	.	.	.	.	.	.	.	.	.	.	.	.,2	.,2	2	2	2,1	.,1
34. male protarsomere 3 shape	.	.	.	.,1	2	.	.	.	.,1	.	.	.	.	.	.	.	.	.
35. protarsomere 4 projection	.	.	1	1	1/.	.	.	.	.	1	.	.	.	.	.	.	.	.
36. flagellar sheath	.	.	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.
45. pillow with scales	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
47. ventral bulge	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.
52. stylomere 2 length	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
53. #dorsolateral sensilla	.	.	.	.	.	.	.,1	O,.	O,.	.	-1	O,.	O,.	.	.	O,.	.	.
54. sternum X setation	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
55. autosome number	.	.		.			.		.	.	2	2	2	2	2	2		
56. Y chromosome size	1	1		.			.		1	1	.	.	1		.,1	.		
58. L, head (other than spots)	2	2	1	1			1		2	.	.	.	.	.	.	.		
59. frontale behind FR,	.	.		O			O		.	1	.	.	.	.	.	.		
60. frontale - anteriorly behind FR,	./1	.		O			O		1	1	1	1	1	1	1	1		
61. parietal eggbursters	.	.		.			1		.	.	.	.	.	.	.	.		
62. pronotum microtubercles	.	.		.			.		.	1	.	.	.	.	.	.		
63. seta FR, width	.	.		.			1		1	.	.	.	.	.	.	.		
64. seta FR, width	.	.		.			1		1	1	.	.	.	.	.	.		

Table 7, *cont'd.*

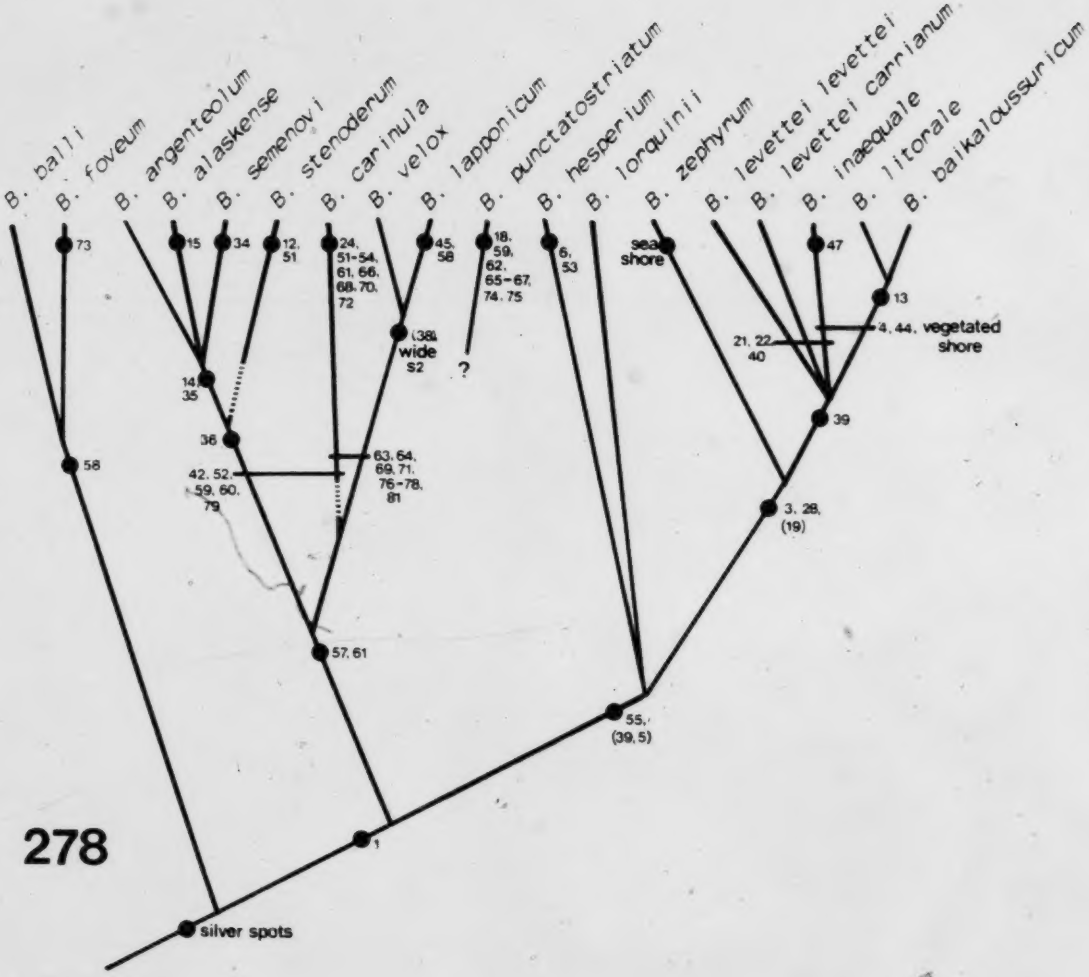
Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	bk
65. seta PR_4 length	.	.		.			.		.	1	.	.	.	.	.	.		
66. seta PR_{10} length	.	.		.			1		.	2	.	.	.	.	.	.		
67. gPR & gME lateral setae	.	.		.			.		.	1	.	.	.	.	.	.		
68. seta PR_{11} size	.	.		.			1		.	.	.	.	.	.	.	.		
69. seta ME_2 length	.	.		.			2		2	1	.	.	.	.	.	.		
70. seta ME_{14} length	.	.	.	.			1		.	.	.	.	.	.	.	.		
71. seta TE_8 length	.	.		.			2		2	1	.	.	.	.	.	.		
72. seta TE_{11} length	.	.	.	.			1		.	.	.	.	.	.	.	.		
73. seta TE_{11} shape	.	1		.					.	.	.	.	.	.	.	.		
74. seta $TE\alpha$ (near TE_8)	.	.		.			.		.	1	.	.	.	.	.	.		
75. seta EP_1 length	.	.		.			.		.	1	.	.	.	.	.	.		
76. segment VIII seta EP_1 width	.	.		.			1		1		.	.	.	.	.	.		
77. seta ST_2 on segment IX	.	1		.			1		1	.	.	.	.	.	.	.		
78. mandible mesal margin	.	.		.			1		1	.	.	.	.	.	.	.		
79. extra setae near FR_3	.			1			1		.	.	.	.	.	.	.	.		
81. # long urogomphus setae	.			.			2		3	.	.	.	.	.	.	.		

To infer clades within *Chrysobracteon*, I examined the data, and attempted to find a phylogeny that would be as consistent as possible with a monophyletic origin of each set of species sharing derived characters of Table 7; that is, I tried to propose as few origins of derived states as possible. I further refined the phylogeny by then incorporating information from all of the other characters. A multistep procedure was used, with cladistic structure slowly being built up, this cladistic structure then allowing me to begin to understand evolution in the initially uninterpretable characters. The procedure used was thus similar to Watrous and Wheeler's (1981) functional outgroup / functional ingroup method. I cannot describe it more explicitly, as it was not done rigorously.

I then reexamined this initial cladogram and tried to improve it by rearranging some of the branches. The resulting phylogeny is presented in Fig. 278. I will now discuss the evidence.

B. balli **and** *B. foveum*. These species are very similar, differing in only 6 of 78 characters of Table 2. However, most of the traits shared appear to be symplesiomorphies. I could only find one trait (dark larval head capsule, character 58) that appears to be a synapomorphy linking them, a state presumably independently derived in *B. lapponicum*. Evidence for their close relationship is thus weak. While I suggest that they may be the primitive sister

Figure 278. Proposed phylogenetic relationships of species of *Chrysobracteon*. Numbers below a clade indicate the characters (from Table 2) that provide evidence for the monophyly of that clade. Four character states in addition to those of Table 2 are also included.


B. balli
B. foveum
B. argenteolum
B. alaskense
B. semenovi
B. stenoderum
B. carinula
B. velox
B. lapponicum
B. punctatostriatum
B. hesperium
B. lorquinii
B. zephyrum
B. levettei levettei
B. levettei carrianum
B. inaequale
B. litorale
B. baikaloussuricum
73
15
34
12, 51
24, 51-54, 61, 66, 68, 70, 72
45, 58
18, 59, 62, 65-67, 74, 75
6, 53
sea shore
47
13
4, 44, vegetated shore
21, 22, 40
(38), wide, 52
?
14, 35
36
58
42, 52, 59, 60, 79
63, 64, 69, 71, 76-78, 81
39
3, 28, (19)
57, 61
55, (39, 5)
1
silver spots

278

group to the rest of *Chrysobracteon*, it is possible that they form a primitive paraphyletic grade.

Only one of the species, *B. foveum*, shows an autapomorphy: the bluntly tipped, parallel-sided TE_{11} of abdominal terga of first instar larvae (Fig. 249, character 73).

***Chrysobracteon* excluding *B. balli* and *B. foveum*.** Uniting this group is one derived character state, presence of distinct mirrors on elytral interval 3 (character 1); this is thus the "mirrored clade" of *Chrysobracteon*. Mirrors are unique within the *Odontium* subgeneric group, and to my knowledge are repeated only in distantly related subgenus *Notaphiellus* among *Bembidion*.

***B. argenteolum*-subgroup.** *B. argenteolum*, *B. alaskense*, and *B. semenovi* share two derived features of protarsomere 4: the ventroapical projection is absent or essentially so (character 35), and the associated setae are less flattened than in other *Chrysobracteon* (character 14). (The possession of these traits by *B. punctatostriatum* will be discussed later.) Note that both of these are relatively low-weight characters (Table 3), in part because of the difficulty I had in observing their states. As well, the characters may be functionally related, and may not evolve independently (both belong to dependency group 2, Table 3); the two states may only provide one piece of evidence. However, as there is no compelling evidence against the union of these three similar species, I will treat them as forming a monophyletic group.

Within the subgroup, *B. alaskense* is autapomorphic in having widely separated ventroapical setae of protarsomere 4 (Fig. 92, character 15). I have seen similarly separated setae in *B. interventor* (Fig. 91), *B. quadrimaculatum*, and *Asaphidion alaskanum* (Fig. 90), but I have doubts that the widely separated setae of these species are homologous to the setae of *B. alaskense*. Even if the setae were homologous, I believe the state in *B. alaskense* to be independently derived from that of distantly related *Bembidion* and *Asaphidion*. To presume otherwise would imply numerous derivations of closely set setae, or a rearrangement of the cladistic structure to unite *B. interventor*, *B. quadrimaculatum*, *Asaphidion alaskanum*, and *B. alaskense* as close relatives; but the latter would force many extra steps into the hypotheses of evolution of other characters.

The holotype of *B. semenovi* also possesses one autapomorphy, the prominent lateroapical projection of male protarsomere 3 (Fig. 78, character 34). This is not an easily interpretable character (states are difficult to distinguish without SEM work), and further examination may reveal a lack of distinctiveness of the state in *B. semenovi*.

The interrelationships within this subgroup are unclear; I found no characters that would allow me to resolve its cladistic structure, if it is to be resolved further.

B. stenoderum. This is a somewhat enigmatic species. I have tentatively placed it as the sister group of the *B. argenteolum*-subgroup, but the evidence is weak. The only uniquely derived state linking the groups is the presence of a dark and ventrally hooked flagellar sheath (character 36, visible in Figs. 114 to 116; basic weight of 0.8). The common presence of a relatively small ostial microtrichial patch (character 42) is also suggestive, but I am not as convinced that the traits of *B. stenoderum* and the *B. argenteolum*-subgroup are derived. Ostial microtrichial patches in *B. carinula*, four *Odontium* species, and several more distantly related *Bembidion* are also small or absent (Tables 2, 4, and 5), throwing doubts upon the use of the character as evidence linking *B. stenoderum* and the *B. argenteolum*-subgroup.

B. stenoderum itself possesses two autapomorphies: exceptionally long S1 setae (character 51), and presence of two elytral ed7 setae instead of just one. Long S1 setae have arisen independently in the stock leading to *Pseudoperyphus* and *B. concolor* . Two ed7 setae are, however, unique among examined Bembidiina.

B. velox and *B. lapponicum*. The placement of *B. velox* with *B. lapponicum* is only weakly supported by character 38 (a distinctly ridged right CSC lobe of the male internal sac), a character of low weight. If I am correct in presuming this is a synapomorphy of the two species, then the trait was independently derived in *B. stenoderum* and *B. lorquinii*. Placing *B. velox* with *B. stenoderum* would yield a conflict in character 36, and with *B. lorquinii* a conflict in characters 39 and 55, whereas the present grouping with *B. lapponicum* is conflict-free. Some additional evidence for the placement of *B. velox* is the relatively wide female second stylomeres, a trait derived within *Chrysobracteon*, shared with *B. lapponicum* (Figs. 155 and 156). The width/length ratio of *B. lapponicum* is .42 (n=1), for *B. velox* .47 (n=1); the next widest *Chrysobracteon* is *B. lorquinii*, with .40 (n=1); other *Chrysobracteon* are all less than .37 (1-2 specimens from each of 13 species measured). The relationships of *B. velox* will probably remain in doubt until first instar larvae are known.

B. lapponicum is characterized by two autapomorphic features, namely presence of a "pillow" on the male internal sac clothed with large scales (Fig. 119; character 45), a trait not found in other *Bembidion*, and a dark larval head capsule (character 58). The dark larva is apparently convergent with that of *B. balli* and *B. foveum*.

B. carinula. As for *B. stenoderum* and *B. velox*, the placement of *B. carinula* is somewhat of a mystery, but in this case the mystery arises from too much conflicting evidence rather than not enough. *B. carinula* shares eight derived larval characters with *B. lapponicum*, all (except 78, presence of a wide shelf on the mesal margin of mandibles) setal, including five full-weight characters (Table 3). However, this suite of setal characters may belong to a functional complex and may not evolve independently; they may not represent seven different lines of evidence. Pleiotropy may also account for some of the coincidence of derived states: characters 63, 64, and 76 all involve a widening of setae; characters 69 and 71 a shortening of setae; characters 77 and 81 an increase in number of setae. These seven characters may involve only three genetic systems; but at present this is unsupported speculation. *B. carinula* shares with the *B. argenteolum*-subgroup a relatively small ostial microtrichial patch of male genitalia (character 42), long female S2 (character 52), and three derived larval characters (microsculptural: characters 59, 60; setal: character 79); the latter two are lower weight. These characters may be more independent than those linking *B. carinula* with *B. lapponicum*, but I am less sure of their polarity within *Chrysobracteon*. As well, joining *B. carinula* with the *B. argenteolum*-subgroup would conflict with a single origin of the hooked flagellar sheath of *B. argenteolum*-subgroup + *B. stenoderum* (see discussion above under "*B. stenoderum*"). The weight of the evidence sways me to place *B. carinula* tentatively with *B. velox* and *B. lapponicum*.

B. carinula boasts an impressive array of ten autapomorphic traits (one of adult pronota (character 24), four of female genitalia (characters 51-54), and five larval (characters 61, 66, 68, 70, 72)). Most spectacular among these are the elongate female second stylomeres (Fig. 154) and the large parietal egg bursters of first instar larvae (Figs. 228 and 234).

B. argenteolum-**subgroup +** *B. stenoderum* + *B. carinula* + *B. velox* + *B. lapponicum*. Evidence for the monophyly of this group comes from first instar larval characters of four species with known larvae (*B. argenteolum*, *B. alaskense*, *B. carinula*, and *B. lapponicum*). All are lacking the three-spotted frontale characteristic of the *Odontium* subgeneric-group (character 57), and the latter three species have exceptionally large parietal egg bursters, reaching an extreme in *B. carinula* (state in *B. argenteolum* unknown). As discussed earlier, these may be correlated developments, with an increase of egg-bursting function by the parietale going hand-in-hand with a decrease in frontal microsculpture and pigmentation. Other common traits of members of the group (most notably the lack of extensive mirror development anteriorly and on the outer elytral intervals) are apparently symplesiomorphies.

Remaining *Chrysobracteon*, **excluding** *B. punctatostriatum*: *B. hesperium* + *B. lorquinii* + *B. inaequale*-subgroup. The only clearly derived character indicating a common origin of members of this clade is the low chromosome number: 2n=20+XY (character 55). Chromosome number is relatively stable within *Bembidion* (Maddison 1985), and thus presumably evolves relatively slowly. While *B. nebraskense* LeConte is also 2n=20+XY, the primitive state in *Chrysobracteon* is most likely 2n=22+XY (Maddison 1985; see that paper for a further discussion of evolution of this character within *Chrysobracteon* and *Bembidion*). Weaker evidence is provided by the expansion of the silver spots onto the interval 5 (character 5) in some members of all species; this character is highly polymorphic within species, however, and is probably not trustworthy. The at-least-slightly angled VSP dorsal ridge in the male internal sac (character 39) may also be a synapomorphy of the group. This is probably a monophyletic group; its unity is threatened primarily by *B. punctatostriatum* (to be discussed in detail later).

Within the group, there are relatively few derived character states, and several unresolved multichotomies.

B. inaequale-**subgroup.** Members of this subgroup possess the most extensive development of mirrors of any *Chrysobracteon*: in addition to inner mirrors, distinctive mirrors are present on intervals 6 and 7 (character 3), as well as anteriorly on intervals 3 to 5. All contained taxa have as well at least some members with sinuate interneur 4 (character 28), and all (except *B. litorale*, presumably through secondary loss) have a rectangular mentum tooth with deep lateral incisions (character 19); only the latter is a full weight character. These states are all derived, and indicate the probable monophyly of the *B. inaequale*-subgroup.

B. hesperium **and** *B. lorquinii*. These species do not possess the autapomorphies of the preceding subgroup, and thus one or both of them probably form its sister group; but I don't know which. I do not have evidence that would allow me to resolve the trichotomy.

Among the 81 characters, *B. hesperium* is autapomorphic in generally possessing transverse elytral sculpticells, a feature independently derived in a large number of other carabid groups. Females of the species also lack dorsolateral ensiform setae of second stylomeres (Fig. 157; character 53).

B. levettei + *B. inaequale* + *B. litorale* + *B. baikaloussuricum*. These taxa share the derived condition of a sharply angled VSP dorsal ridge in the male internal sac (character 39), a feature shared among the *Bembidion* that I have studied only with *B. (Odontium) durangoense*. I tentatively conclude that they form a monophyletic group. This leaves *B. zephyrum* as their sister group.

B. zephyrum. I know of no structural autapomorphy of this species among the 81 characters of Table 2; however, the seaside habitat of members of this species is undoubtably a derived feature (a behabvioral autapomorphy) of *B. zephyrum* alone.

B. levettei. I have no evidence that *B. levettei levettei* + *B. levettei carrianum* form a monophyletic unit.

B. litorale **and** *B. baikaloussuricum*. The exceptionally narrow male adhesive setae suggests relationship of these two species (character 13). They also have relatively narrow male protarsomere 1's (Fig. 86), which I presume to be derived, but I have not studied the character in enough detail to be sure.

Relationships of *B. inaequale*. There is conflicting evidence regarding the placement of *B. inaequale*. Two mouthpart characters (21 and 22) suggest relationship with *B. levettei*, as does the scaled VSP dorsal ridge (character 40). The latter trait, while occurring in a few of the less-mirrored *Chrysobracteon*, is in those species of a different nature than in *B. inaequale* and *B. levettei*. In *B. balli*, *B. foveum*, and the *B. argenteolum*-subgroup, the scales are dense and platelike; in *B. inaequale* and *B. levettei* the scales are sparse and ridgelike. Both scale types occur outside of *Chrysobracteon*, and thus the character is subject to convergence. However, other characteristics of *B. inaequale* and *B. levettei*, the isolated outer mirrors (character 4) and sclerotized ostial strip of the internal sac (character 44), indicate placement with the *B. litorale* + *B. baikaloussuricum* line. Further support for the *B. litorale* + *B. baikaloussuricum* connection is the occurrence of both *B. inaequale* and *B. litorale* on sparsely vegetated shores; other *Odontium*-subgeneric group members occur on mostly barren soil, and the condition of *B. inaequale* and *B. litorale* is presumably derived.

I do not feel that the evidence weighs heavily in either direction; for the moment I leave an unresolved multichotomy. Which ever way it will eventually be resolved, hypotheses of parallelism or convergence will be required.

One trait may be an autapmorphy of *B. inaequale*, the large ventral bulge of male aedeagi (character 47), a state independently derived in *B. (Pseudoperyphus) honestum*.

Placement of *B. punctatostriatum*. *B. punctatostriatum* has proved to be the most troublesome species to place. Its members share derived characters with three separate lines, and I do not choose between the possible placements. Protarsomere 4 of *B. punctatostriatum* is similar to the derived articles of the *B. argenteolum*-subgroup (characters 14 and 35, both with basic weights of 0.8), and the excessive elytral setae between eo4 and eo5 also links the species to *B. argenteolum* and *B. semenovi*; but placing *B. punctatostriatum* with the *B. argenteolum*-subgroup would force a more complicated hypothesis of flagellar sheath (character 36) evolution. The larvae of *B. punctatostriatum* share four derived characters with *B. lapponicum* (characters 64, 69, 66, and 71; all setal, basic weights 0.8 except 64, with weight=1.0); but placing *B. punctatostriatum* with *B. lapponicum* would cause conflicts within larval characters

57 and 61. The mentum of *B. punctatostriatum* is very similar to the derived mentum of *B. inaequale* and *B. levettei* (Figs. 52 and 55; characters 19, 21, and 22, all full-weight), but similar menta are found in *B. cheyennense* (Fig. 57), *B. confusum*, and *B. umbratum*. As well, placing *B. punctatostriatum* with these species would lead to conflicts in characters 3, 27, and 55.

I simply cannot place *B. punctatostriatum*, and leave it within mirrored *Chrysobracteon* unconnected to any lineage (Fig. 278).

It is possible, although unlikely, that the mixed features of *B. punctatostriatum* are a result of a hybrid origin of the species or its ancestors. However, the evidence from other characters of hybridization between extant *Bembidion* lineages is meager or non-existent, and I think it simpler to presume independent evolution of features rather than multiple cladistic reticulation.

B. punctatostriatum, like *B. carinula*, possesses a number of autapomorphies. *B. punctatostriatum* has derived states of characters 18 (adult lacinia shape), as well as 59, 62, 65-67, 74, and 75 (all larval). All except the extensive frontale microsculpture (character 59) have arisen independently in more distantly related Bembidiina. Most striking is the convergence in larval characters between *B. punctatostriatum* and *Asaphidion alaskanum*. Both possess widespread pronotal microtubercles, setal groups gPR and gME (Fig. 237, 241), and relatively short setae EP_1 (characters

59, 67, and 75). The larvae are otherwise quite dissimilar, and their distant relationship precludes a common origin of the three larval traits.

5.5.2 Certainty of the reconstructed phylogeny

How much confidence can be placed in the reconstructed phylogeny? Not much, I think.

First, the data set is very complex. Most of the 81 characters studied showed independent derivation of traits in *Chrysobracteon* and the outgroups. There was a great deal of conflict between the characters within *Chrysobracteon* and outside of it. One outgroup species, *B. cheyennense*, illustrates this quite well. In the scheme I have presented, *B. cheyennense* is cladistically an *Ochthedromus*, and not a *Chrysobracteon*, and yet its ancestors have acquired a number of states independently from those of *Chrysobracteon* species. The faintly mirrored elytra, bulbous and rectangular mentum tooth, short larval setae PR_{10}, TE_6, and microtubercled first instar pronota are all presumably convergent with similar states in *Chrysobracteon* species such as *B. punctatostriatum*, *B. levettei*, and *B. carinula*.

If characters evolved slowly, one would expect repetitious, nested patterns of shared derived characters; the patterns in *Chrysobracteon* are clearly not well-nested. It thus seems that the character states I examined in *Bembidion* are not good indicators of phylogeny. As well, because of the confusion in the data, patterns were not clearly evident to me, and I do not feel confident that my mind was capable of properly balancing the complexity.

I must say, however, that there is hope, as I do not feel I have as yet extracted all of the evidence from the data presented. This may come with the numerical analysis.

There are also several technical problems with my approach. First, I did not consider character interaction in my outgroup analysis (Maddison *et al.* 1984). Second, I used sequential rather than simultaneous resolution of the ingroup: cladistic structure I assumed along the way may have steered me away from the global optimum. I may have been led down the wrong path by initially promising choices. Third, I didn't use all of the information in the outgroups. The reasons for the lack of unequivocal ancestral state assessments during outgroup analysis were the ignorance of outgroup cladistic structure and the variation, within the outgroups, of the characters used to resolve *Chrysobracteon* phylogeny. But these characters could themselves be used to help resolve the outgroups. If I had inferred outgroup structure using all characters that varied within the outgroups (and not just the few mentioned under "Cladistic structure of near relatives of *Chrysobracteon*"), then perhaps more definitive assessments of ancestral states would have been obtained, and *Chrysobracteon* phylogeny would be more fully resolved.

The best way to handle the data would have been to simultaneously resolve the outgroups plus the ingroup with information from all 81 characters, with more rigorous means of choosing between conflicting hypotheses. Such a task is beyond my mental capabilities, and for this a computer program such as PAUP is required.

5.5.3 Reanalysis considering dependency groups

The "altered weight" of Table 3, which incorporated information about dependency groups, was primarily intended for the numerical analysis, as the full effect of the weights I find difficult to sort out mentally. Nonetheless, a brief mental analysis considering these altered weights is useful.

The most striking effect of this is to lower the weights of the male genitalic characters, although only a few characters survive unscathed (Table 3).

Under these altered weights, I would still place *B. carinula* with *B. lapponicum* and *B. velox*, as with these it shares derived states of characters of altered weights 0.7, 0.7, 0.5, 0.5, 0.7, 1.0, 0.8, and 1.0, whereas with the *B. argenteolum*-subgroup weights of the uniting characters are 0.5, 0.6, 0.7, 0.5, and 0.8.

Relatives of the other problematic species, *B. punctatostriatum*, are still no more apparent under the altered weights. *B. punctatostriatum* shares with the *B. argenteolum*-subgroup apomorphies in characters of weights: 0.5 and 0.5; with *B. lapponicum*: 0.7, 0.5, 0.3, and 0.5; with *B. inaequale* and *B. levettei*: 0.6, 0.6, and 0.6.

Again I hesitate to connect it with any specific lineage of mirrored *Chrysobracteon*.

In using these altered weights, one presumes that the characters belonging to one dependency group evolve in concert. However, the data at hand cast doubt upon this notion, as variation of characters within a dependency group is not perfectly correlated (see, for example, conflicts in distribution of the male genitalic characters of dependency group 9). The analysis using only basic weights is perhaps more appropriate.

5.5.4 Numerical Analysis

In the published version of the present work, numerical cladistic analyses, conducted in part with PAUP, will be included. All 81 characters and 56 taxa (*Chrysobracteon* plus all studied outgroups) will be incorporated. Included will be analyses with: (1) all outgroup structure as for mental analysis, with characters weighted according to "basic weight" of Table 3; (2) all outgroup structure as for mental analysis, with characters weighted according to "altered weight" of Table 3; (3) no outgroup structure assumed, except for monophyly of *Chrysobracteon*, the *Odontium* subgeneric group, and *Bembidion*, with characters weighted according to "basic weight" of Table 3; (4) no cladistic structure assumed initially (not even the monophyly of *Chrysobracteon*), with characters weighted according to "basic weight" of Table 3; (5) no cladistic structure assumed beforehand and characters weighted equally.

5.6 Fossil Material

The oldest *Chrysobracteon* fossils are fragments from the Beaufort Formation of Banks and Meighen islands. They are apparently middle to late Miocene, approximately 7-13 million years before the present (Matthews 1976, 1977, 1979). I have examined 14 of these fragments (JVMa!), identifiable with some certainty as *Chrysobracteon*. Character states of these pieces are shown in Table 8.

Unfortunately, exact placement of any of these specimens on the phylogeny of Fig. 278 is impossible, due to the lack of visible character states. Nonetheless, some assignments can be made.

For example, specimen B7 from Banks Island (JVM 3-73) is clearly a fragment of a *Chrysobracteon* elytron (as a silver spot is present), but third interval elytral mirrors are lacking. The specimen thus belongs to the *B. balli*-*B. foveum* line, the stem-group of the rest of *Chrysobracteon* (from a lineage predating the evolution of mirrors), or from the stem-group of *Chrysobracteon*.

Some of the other elytral fragments possess mirrors, and thus belong to the "mirrored clade" of *Chrysobracteon*. Placement beyond this is difficult, and of questionable validity. The specimens are phenetically most similar in visible features to *B. levettei*, but many of these similarities are symplesiomorphies. Cladistically they could fall nearly anywhere within the mirrored *Chrysobracteon*.

Table 8. Character states of Miocene Beaufort Formation *Chrysobracteon* **fossils.**

Lot number JVM 3-73 is from Banks Island; all the rest are from Meighen Island.

Numbers in front of characters are those from Table 2. For numbered characters, state code matches those in Table 2; for others, code as follows: **body part**: E: elytron, P: pronotum; **silver spots?**: Y: yes, N: no; **3rd interval width**: W: distinctly wider than 2nd, N: as wide as second; **ed5 pit shape**: C: circular.

	LOT NUMBER and *SPECIMEN NUMBER*													
	JVM 3-73						**JVM 5-73**		**Columbia Bridge**		**MRA 8-3-75-1**	**MRA 8-1-75-4**		
Character	*B2*	*B3*	*B4*	*B5*	*B6*	*B7*	*B3*	*B5*	*A1*	*A2*	*B4*	*A4*	*A5*	*B5*
body part	E	E	E	E	E	E	E	P	E	E	E	P	P	E
silver spots?	Y	Y	Y	Y	Y	Y	Y		Y	?	Y			Y
1.mirrors on 3rd?	Y	Y	Y			N	Y		Y		Y			Y
2.mirrors on 4&5th?	Y	Y	Y			N	Y							Y
6.sculpticell shape	I	I	I	I	I	I	I		I		I			I
8.midlateral seta								1				1	1	
9.ed3/5 & interneur	F	F	F	F	F	F	F		F	F	F			F
10.ed3/5 & silver spot	A	A	A	A	A	A			A/C		A		A	
24.pronotal carina								1				O	1	
27.humeral margin		S	S/M		S				M	S	S/M			
28.interneur 4 straight?									Y	Y	Y			
interval 3 width	W	W	W	W	W	W	W		W		W			W
ed5 pit shape						C								

The most notable features of the three pronota are a lack of a long basilateral carina, and presence of midlateral setae. There are a number of *Chrysobracteon* lineages to which they might belong. As with the elytral fragments, the known pronota unfortunately contribute scant information about *Chrysobracteon* evolution.

A few Pleistocene fragments have also been discovered. The only specimen from North America with which I am familiar is an elytron, probably of *B. levettei*, from southern Ontario; this specimen is from well within the range of present day. *B. levettei*.

Coope (1969, 1979b) reports *B. velox* from Late Würm Glacial (Zone I) and Early Windermere Interstadial (13,200-12,000 years b.p.) deposits in Britain. This species is not extant in Britain, although it occurs across the English Channel in France (Fig. 266). From Glacial sediments just predating the Windemere Interstadial of the Isle of Man (about 19,000 years b.p.), fragments of *B. lapponicum* have been discovered (Coope 1977, 1979a). *B. lapponicum* is now absent from the British Isles, occurring now in northern Scandinavia (Fig. 267); its presence 19,000 years ago in Britain reflects the cooler climate at the time (Coope 1977, 1979a). *B. litorale* is known from Early Windermere Interstadial (13,200-12,000 years b.p.) deposits in the British Isles (Coope 1979b); this is within the modern geographic distribution of the species.

The Pleistocene material, therefore, contains extant species in not-unexpected localities.

5.7 General patterns of evolution in *Chrysobracteon*

A few general patterns in the data are worthy of note and discussion. The patterns pose more questions than they answer, and are noted here more for incentive they may provide for future research, than for the conclusions they yield.

Most of the species possessing autapomorphies are among the *Chrysobracteon* without extensive mirrors (Fig. 278). The clade with extensively mirrored members, the *B. inaequale*-subgroup, contains only one species (*B. inaequale*) among five with a detectable structural autapomorphy (although *B. zephyrum* has uniquely invaded the seashore), whereas among the other *Chrysobracteon* seven of eleven species are autapomorphic in at least one character. The significance of this eludes me. It could mean that the *B. inaequale*-subgroup has undergone speciation relatively recently, so that species are too young to have gained many distinctive traits, while splits between the other *Chrysobracteon* may be relatively ancient. Alternatively, the other *Chrysobracteon* may have higher rates of evolution in the characters studied, and the lineage splits may be of comparable age to that in the *B. inaequale*-subgroup. At present I cannot choose between these hypotheses.

5.7.1 Evolution of mirrors

A most noticeable feature of many adult *Chrysobracteon* is the presence of elytral mirrors. Why mirrors evolved is a puzzle. The mosaic pattern created by the mirrors is similar to that produced by pigment in other *Bembidion* (for example, many members of *Notaphus*). Microsculpturally mosaic elytra have evolved independently a number of times in caraboids (a few examples are *Systolosoma*, *Elaphrus*, *Opisthius*, *Scopodes*, and *Asaphidion*). Perhaps the mosaic pattern confuses potential predators; at least in humans, "these patches tend to catch the eye of the observer and to draw his attention away from the shape which bears them" (Cott 1940:48). Or perhaps mirrors are for thermoregulatory purposes; or perhaps there is some other function (see Lindroth 1974b).

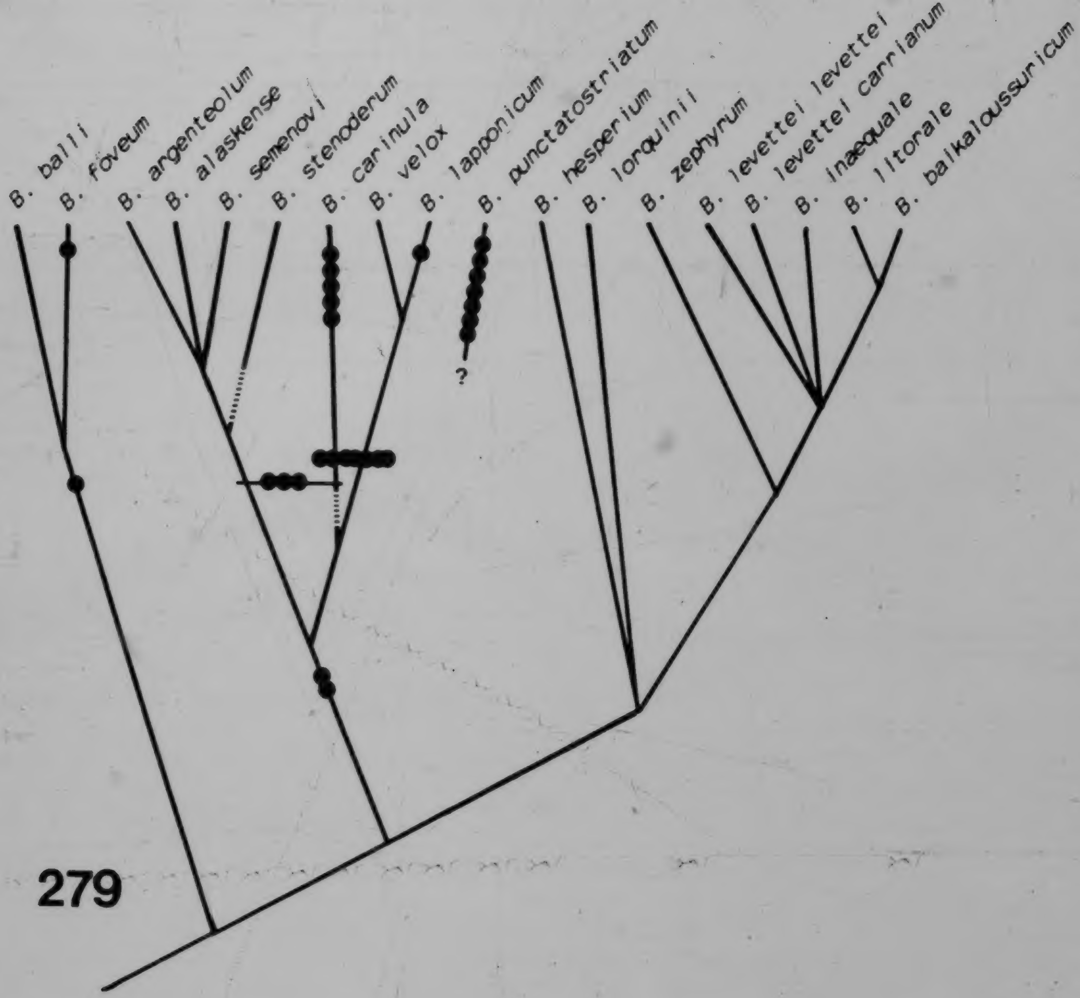
In his study of *Elaphrus*, Goulet (1983) notes a striking correlation between overall shininess of the beetles and substrate moisture, with shinier beetles occurring on wetter soils; as well, more extensively mirrored *Elaphrus* tend to occur on wetter substrates. Within *Chrysobracteon*, the limited knowledge I have of habitats reveals no correlation between microsculpture and substrate. For example, unmirrored, dull beetles such as *B. foveum* and *B. balli* coexist in the same microhabitat with extensively mirrored, relatively shiny species such as *B. levettei*. Goulet (1983) explains the patterns he notes as resulting from evolutionary development of crypsis in response to predation; clearly, no such explanation is readily available for *Chrysobracteon*. I cannot think of adaptive reasons for the divergence on microsculpture.

5.7.2 Evolution of larvae

The most primitive larvae of *Chrysobracteon* are found in the clade with 20 autosomes (*B. hesperium* + *B. lorquinii* + *B. inaequale*-subgroup). Almost all of the evolution of larvae of *Chrysobracteon* has taken place within the less-mirrored members of the mirrored clade (Fig. 279). Again, it is difficult to select any specific hypothesis explaining this pattern without more basic data about the lifestyles of *Chrysobracteon* species.

One notable correlate is the presence in *B. carinula* of both the longest second stylomeres (Fig. 154) the largest egg bursters (Figs. 228 and 234) of any *Odontium* subgeneric group members. Perhaps the long S2's are suited for laying eggs in an unusual microhabitat, a place that requires tougher chorion, which in turn requires larger egg bursters. A comparative study of the habits of *B. carinula* and related species could provide a most rewarding test of this hypothesis.

Figure 279. Distribution of derived larval states in *Chrysobracteon*. Each dot represents the hypothesized origin of one larval state.


B. balli
B. foveum
B. argenteolum
B. alaskense
B. semenovi
B. stenoderum
B. carinula
B. velox
B. lapponicum
B. punctatostriatum
B. hesperium
B. lorquinii
B. zephyrum
B. levettei levettei
B. levettei carrianum
B. inaequale
B. litorale
B. baikaloussuricum
?

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6. HISTORICAL MOVEMENTS OF *CHRYSOBRACTEON* LINEAGES

6.1 Methods

As with phylogeny reconstruction, historical biogeography can be approached either from a likelihood or parsimony perspective. One could produce maximum likelihood estimates of the biogeographic history of a group, if one built a general model of the biogeographic behavior of lineages of the animals, and used it with presumed phylogenetic and geologic history. This would involve background assumptions.about the dispersal abilities, natural history, etc., of the organisms. Such an analysis could be conducted mentally or numerically. To my knowledge, numerical biogeographic methods for single clades (as opposed to whole biotas (Rosen 1978, Simberloff *et al.* 1981)) remain wholly undeveloped. The reasons for this probably include the mathematical difficulties involved, as well as the lack for most groups of sufficient knowledge necessary to apply such techniques.

Such methods would undoubtedly be opposed by those cladists seeking to produce patterns using a minimum of process hypotheses; they would instead use vicariance biogeographic techniques. Vicariists choose those hypotheses that invoke vicariance as much as possible, and dispersal as little as possible, in explaining geographic distributions. This is considered by its practictioners to be a parsimony method, as the number of hypothesized dispersal events is minimized.

I will not embark on a critique of either approach, something I am not fully capable of doing at present. The methods I use are a mental amalgam of likelihood and parsimony techniques, and as such are rather ill-defined.

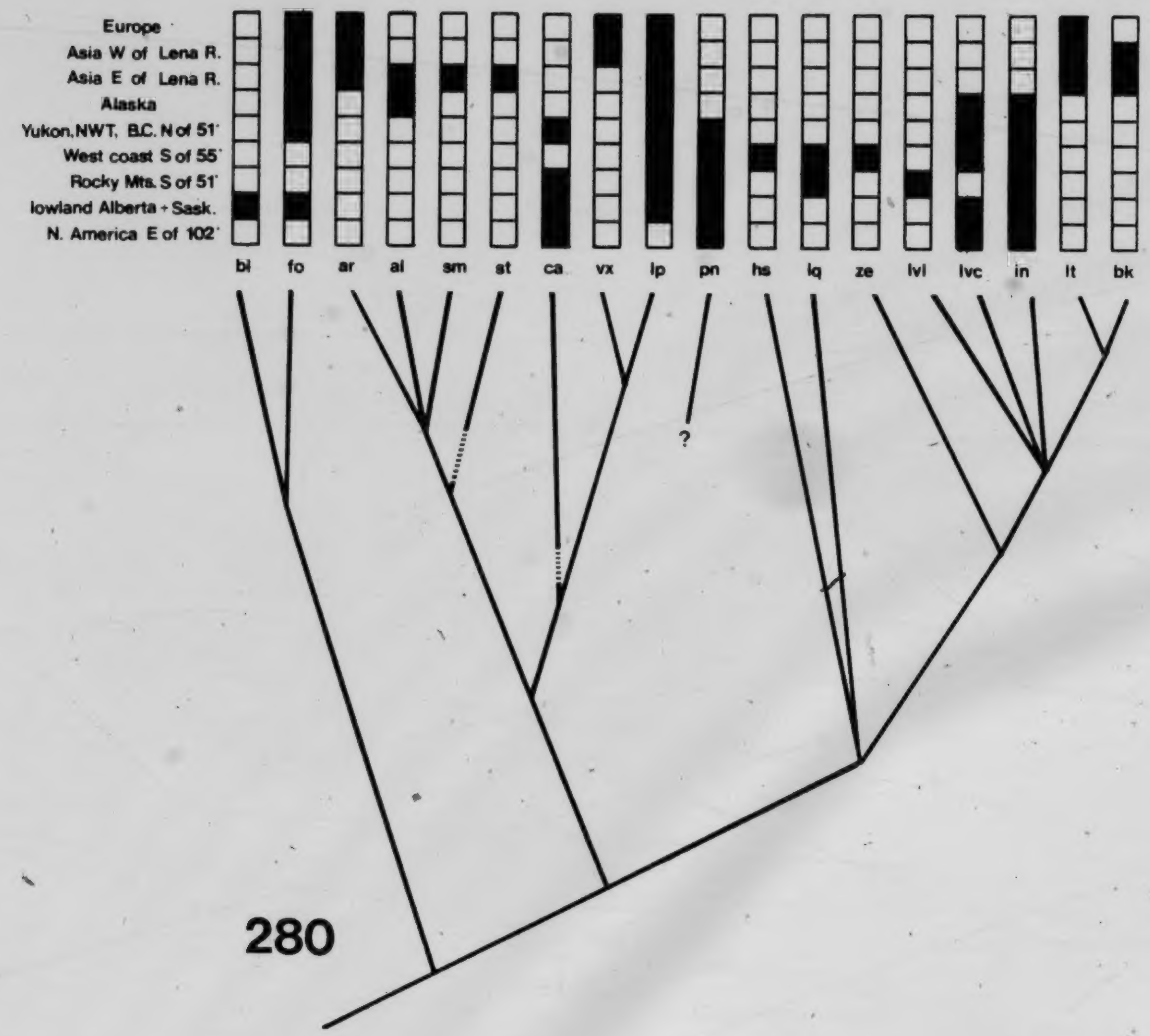
6.2 Geographic history of *Chrysobracteon* lineages

I have examined the geographic history of *Chrysobracteon* only cursorily, and present herein a few thoughts on the subject.

As can be seen from the distribution maps (Figs. 261-274) and Fig. 280, many *Chrysobracteon* are widespread with coincident ranges. For example, within the Nearctic region, *B. carinula*, *B. punctatostriatum*, *B. levettei*, and *B. inaequale* are all transamerican, from the Yukon Territory south into the contiguous United States. Dispersal has undoubtedly played a prominent role in the history of *Chrysobracteon*, and has resulted in the sympatry (Table 1) and wide ranges of most of the taxa. As well, this expansion of species ranges has probably led to a clouding of vicariant patterns. One can thus expect only a few fragments of the geographic history of these widespread, lowland forms to be detectable. Ecological requirements of *Chrysobracteon* lineages, when more thoroughly known, might provide additional clues.

Eight of the 18 taxa have restricted distributions (*B. balli*, *B. semenovi*, *B. stenoderum*, *B. hesperium*,

Figure 280. Geographic distributions of *Chrysobracteon* species superimposed upon the proposed phylogeny. Abbreviations of taxa names as in Table 2.


Europe
Asia W of Lena R.
Asia E of Lena R.
Alaska
Yukon, NWT, B.C. N of 51°
West coast S of 55°
Rocky Mts. S of 51°
lowland Alberta + Sask.
N. America E of 102°
bl
fo
ar
al
sm
st
ca
vx
lp
pn
hs
lq
ze
lvl
lvc
in
lt
bk
?

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B. lorquinii, *B. zephyrum*, *B. levettei levettei*, and *B. baikaloussuricum*). Four of these, *B. balli*, *B. semenovi*, *B. stenoderum*, and *B. baikaloussuricum* are all near edge of the range of their widespread sister-groups.

B. balli occupies a small area in Alberta and Saskatchewan, just within the southernmost limit of the range of *B. foveum*. A relatively recent vicariance event may have split the common ancestor of these two species, with subsequent dispersal of one or both forms until *B. foveum* attained sympatry with *B. balli*. *B. foveum* populations presumably spent Quaternary glaciations in Nearctic Beringia or in the Palearctic, although they may have been south of the ice sheets in North America. However, it does seem most reasonable that *B. balli* occurred south of the ice sheets, with invasion northward upon glacial retreat. Indeed, the ice sheets may have been the barrier that allowed differentiation of the ancestral *B. foveum*-*B. balli* stock into the two extant species.

B. semenovi is only known from the holotype, found in a region which has been scantily collected. The full range of the species is unknown, and thus biogeographic hypotheses about the species must be considered tentative. Nonetheless, it does seem reasonable to presume an isolation of a southern portion of the proto-*B. argenteolum*-*B. semenovi* stock resulting in divergence and separation of *B. argenteolum* and *B. semenovi*. An earlier, later, or contemporaneous east-west vicariance probably resulted in the production of the *B. alaskense* lineage. The lack of cladistic resolution of the *B. argenteolum*-subgroup (Fig. 278) may be indicative of an actual trichotomy, that is, a simultaneous formation of the *B. semenovi* and *B. alaskense* lineages.

A earlier vicariance may have resulted in the formation of *B. stenoderum* from a far eastern isolate of the *B. argenteolum*-subgroup ancestor.

The split between *B. carinula* and *B. velox*-*B. lapponicum* may have been a Nearctic-Palearctic vicariance, with subsequent division of the Palearctic lineage into a western *B. velox* and eastern *B. lapponicum*. More recently, probably in the Pleistocene, *B. lapponicum* invaded North America.

The 2n=20+XY clade originated in the Nearctic, with most of its history in that region. Only relatively recently has one of its stocks (*B. litorale*-*B. baikaloussuricum*) invaded the Old World, with subsequent differentiation of eastern *B. baikaloussuricum* from western *B. litorale*.

The three primitive species of the 2n=20+XY clade (*B. hesperium*, *B. lorquinii*, and *B. zephyrum*) are isolated in western North America from British Columbia south to California, whereas the derived members of the *B. inaequale*-subgroup are more widespread in the eastern and northern Nearctic, and Palearctic (Fig. 280). The Pacific coastal forms may have arisen as buddings from a more widespread Nearctic stock, with one of the buddings (that leading to *B. zephyrum*) invading the seashore. However, a full explanation of this pattern awaits a resolution of their relationships.

6.3 Origin of *Chrysobracteon*

The relatives of *Chrysobracteon*, *Odontium* and *Ochthedromus*, are predominantly southern groups. Within both the New and Old World, species of the latter two groups increase in numbers southward, at the expense of *Chrysobracteon* abundance. *Chrysobracteon* are thus more cool-adapted than their relatives, and probably have been throughout their history; whether the entire *Odontium* subgeneric group assemblage orginated as cool or warm adapted animals, I do not know.

Exactly when the ancestor of *Chrysobracteon* arose is a mystery. It clearly was before the Late Miocene; in fact, the mirrored clade was already in existence by then. I hesitate to speculate age of origin, because of the lack of an adequate fossil record, and the lack of well-supported detailed biogeographic hypotheses.

7. CONCLUSIONS

7.1 On the lack of a definitive reconstructed phylogeny

I have presented a large amount of data about *Chrysobracteon*, and yet I have chosen to come to relatively few conclusions about the history of the subgenus. At times I paint a rather pessimistic picture of the capabilities of the data at hand to help answer the questions of interest. I actually do view the data as providing few clues, as the conflicts and contradictions in it are numerous. I must note, however, that I do not believe that my analysis has extracted all available information from the data set. Along with my reluctance to accept *a priori* background assumptions that would help provide more definite answers, this leads to my conclusions being uncertain.

Weakly supported hypotheses, presented in the name of Popperian science as hypotheses to test, can be easily transformed through the literature into confidently accepted notions. Rather than presenting one fully resolved notion of *Chrysobracteon* phylogeny as an hypothesis, I prefer to express my uncertainty, thus providing a number of hypotheses for future investigators to test, and not just one.

7.2 Directions of future research

Darlington (1970), in his review of the history of *Bembidion* systematics, notes the shift in emphasis from the time of Casey to that of Lindroth. From a view of systematics as a sorting of dead specimens, to Lindroth's studies of populations of living, evolving creatures, the change has encompassed an increasing knowledge of the organisms and their histories. Erwin and Kavanaugh's (1981, in prep.) studies have continued the progress, adding female genitalic characters to our data base, as well as introducing cladistic techniques. I have incorporated more adult structural characters, as well as larval and chromosomal features, along with modified cladistic techniques. But, as always, much remains to be done; a few avenues of research that appear to me to be potentially valuable are worthy of note.

I have only skimmed the surface of geographic variability of *Chrysobracteon* species. *B. inaequale*, *B. lapponicum*, the *B. argenteolum*-subgroup, and *B. litorale*-*B. baikaloussuricum* all require further analysis. A study of external structure variation is warranted, as is that of any other character that might help sort out patterns of gene flow; electrophoresis may be especially useful.

Many more character systems await investigation. One of the most promising avenues of further work on *Chrysobracteon* entails an SEM study of the diversity of microsculpture of male genitalia. The few glimpses I have had of the variation in internal sac surface texture suggests a wealth of hidden information for use in phylogenetic analyses. A study of eggs, third instars, pupae, as well as any of the unstudied characters cited in the section "Character states of *Chrysobracteon*", may prove valuable.

A great aid to a new phylogenetic analysis of *Chrysobracteon* would be a more thorough study of interrelationships of outgroups. Some of the pathways of *Chrysobracteon* evolution may then become clearer.

And last, but not least, more work on the ecological and behavioral characteristics of the species is necessary if we are to meld the phylogenetic analysis more thoroughly with the habits of living creatures.

8. LITERATURE CITED

Ahrens, A. 1812. Beiträge zur Kenntniss deutscher Käfer. **Neueste Schriften der Naturforschenden Gesellschaft zu Halle** 2:1-40.

Ali, H.A. 1967. The higher classification of the Carabidae and the significance of internal chacracters [sic!] (*Coleoptera*). **Bulletin de la Sociétié Entomologique d'Egypte** 51:211-231.

Andersen, J. 1966. The larval stages of the genus *Bembidion* Latr. (Col. Carabidae) I. The larvae of the subgenus *Chrysobracteon* Net. and *B. dentellum* Thunb. **Norsk Entomologisk Tidsskrift** 13:440-453.

____________. 1970. Habitat choice and life history of Bembidiini (Col., Carabidae) on river banks in central and northern Norway. **Norsk Entomologisk Tidsskrift** 17:17-65.

____________. 1978. The influence of the substratum on the habitat selection of Bembidiini (Col., Carabidae). **Norwegian Journal of Entomology** 25:119-138.

Andrewes, H.E. 1921. Notes on Oriental Carabidae—II. Some new species of *Bembidium* from Java and Indo-China. **The Entomologist's Monthly Magazine** 7(third series):248-252.

____________. 1935. **The fauna of British India, including**

Ceylon and Burma. Coleoptera. Carabidae Vol. II. Harpalinae I. Taylor and Francis Publishers, London. 323pp.

Antoine, M. 1955. Coléoptères carabiques du Maroc (Première partie). **Mémoires de la Société des Sciences Naturelles et Physiques du Maroc**. I. 177 pp.

Arnold, E.N. 1981. Estimating phylogenies at low taxonomic levels. **Zeitschrift für zoologische Systematik und Evolutionsforschung** 19:1-35.

Baehr, M. 1979. Vergleichende Untersuchungen am Skelett und an der Coxalmuskulatur des Prothorax de Coleoptera. Ein Beitrag zur Klärung der phylogenetischen Beziehungen der Adephaga (Coleoptera, Insecta). **Zoologica. Originalabhandlungen aus dem Besamtgebiet der Zoologie** 44:1-76.

Ball, G.E. 1972. Classification of the species of the *Harpalus* subgenus *Glanodes* Casey (Carabidae: Coleoptera). **The Coleopterists Bulletin** 26:179-204.

___________. 1975. Pericaline Lebiini: Notes on classification, a synopsis of the New World genera and a revision of the genus *Phloeoxena* Chaudoir (Coleoptera: Carabidae). **Quaestiones Entomologicae** 11:143-242.

___________. 1978. The species of the Neotropical genus

Trichopselaphus Chaudoir (Coleoptera: Carabidae: Harpalini). Classification, phylogeny, and zoogeography. **Quaestiones Entomologicae** 14(4):447-489.

Ball, G.E., and A.P. Nimmo. 1983. Synopsis of the species of subgenus *Progaleritina* Jeannel, including reconstructed phylogeny and geographical history (Coleoptera: Carabidae: *Galerita* Fabricius). **Transactions of the American Entomological Society** 109:295-356.

Ball, G.E., and D. Shpeley. 1983. The species of eucheiloid Pericalina: Classification and evolutionary considerations (Coleoptera: Carabidae: Lebiini). **The Canadian Entomologist** 115:743-806.

Barr, T.C., Jr. 1971. *Micratopus* Casey in the United States (Coleoptera: Carabidae: Bembidiinae). **Psyche** 78:32-37.

Barthe, E. 1912. Tableaux analytiques pour la détermination des Carabidae de la région franco-rhénane, comprenant toutes les espèces, variétés, races et aberrations. **Miscellanea Entomologica. Revue Entomologique Internationale** 20(7):225-240.

Basilewsky, P. 1968. Contributions a l'étude des coléoptères carabiques de la région Malagache. V. Les *Bembidiinae* de Madagascar et des iles voisines. **Annales de la Sociétié Entomologique de France** N.S. 4:515-548.

___________. 1972. La faune terrestre de l'Ile

Sainte-Helene. II.- Insectes. 9. Coleoptera. 1. Fam. Carabidae. **Annales du Musée Royal de l'Afrique Centrale** 192:11-84.

Bates, H.W. 1873. On the geodephagous Coleoptera of Japan. **The Transactions of the Entomological Society of London** 1873:219-322.

____________. 1883. Supplement to the geodephagous Coleoptera of Japan, chiefly from the collection of Mr. George Lewis, made during his second visit, from February 1880, to September, 1881. **The Transactions of the Entomological Society of London** 1883:205-290.

____________. 1891. Additions to the carabideous fauna of Mexico, with remarks on some of the species previously recorded. **The Transactions of the Entomological Society of London** 1891:223-278.

Bauer, T. 1971. Zur Biologie von *Asaphidion flavipes* L. (Col., Carabidae). **Entomologische Zeitschrift** 81:154-164.

____________. 1975. Zur Biologie und Autökologie von *Notiophilus biguttatus* F. und *Bembidion foraminosum* Strm. (Coleopt., Carabidae) als Bewohner ökologisch extremer Standorte. Zum Lebensformtyp des visuell jagenden Räbers unter den Laufkäfern (II). **Zoologischer Anzeiger** 194:305-318.

Beatty, J. 1982. Classes and cladists. **Systematic Zoology** 31:25-34.

Bedel, L. 1879. Faune des coléoptères du bassin de la Seine. **Annales de la Sociétié Entomologique de France**, volume hors série, 1:1-128. [Not seen.]

Bils, W. 1976. Das Abdomende weiblicher, terrestisch lebender Adephaga und seine Bedeutung für die Phylogenie. **Zoomorphologie** 84:113-193.

Boldori, L. 1939. Larve di *Asaphidion* (Coleopt. Carab.). **Bollettino della Societa Entomologica Italiana** 71:98-105.

Bousquet, Y. and H. Goulet. 1984. Notation of primary setae and pores on larvae of Carabidae (Coleoptera: Adephaga). **Canadian Journal of Zoology** 62(4):573-588.

Bøving, A. 1911. Nye bidrag til Carabernes Udviklingshistorie. II. Larver af slægterne *Tachypus*, *Cillenus*, *Trechus*, *Clivina*, *Zabrus*, *Anisodactylus*. **Entomologiske Meddelelser** 4:129-180.

Carr, F.S. 1932. New arctic Coleoptera. **The Canadian Entomologist** 64:191-192.

Casey, T.L. 1918. A review of the North American Bembidiinae. **Memoirs on the Coleoptera** 8:1-223.

___________. 1924. Additions to the known Coleoptera of

North America. **Memoirs on the Coleoptera** 11:1-347.

Cerruti, M. 1939. Larva del *Tachys parvulus* Dej. (Coleop. Carab.). **Memorie della Societa Entomologica Italiana** 17:121-124. [Not seen.]

Chaudoir, M. de. 1868. Observations synonymiques sur les *Carabiques* de l'Amérique septentrionale et descriptions d'espèces nouvelles de ce pays. **Revue et Magazin de Zoologie** 20(second series):239-245.

Clark, W.E. 1978. The weevil genus *Sibinia* Germar: Natural history, taxonomy, phylogeny, and zoogeography, with revision of the New World species (Coleoptera: Curculionidae). **Quaestiones Entomologicae** 14:91-387.

Coope, G.R. 1969. The contribution that the Coleoptera of Glacial Britain could have made to the subsequent colonisation of Scandinavia. **Opuscula Entomologica** 34:95-108.

___________. 1977. Fossil coleopteran assemblages as sensitive indicators of climatic changes during the Devensian (Last) cold stage. **Philosophical Transactions of the Royal Society of London** Series B, 280:313-340.

___________. 1979a. Late Cenozoic fossil Coleoptera: evolution, biogeography, and ecology. **Annual Review of Ecology and Systematics** 10:247-267.

___________. 1979b. The Carabidae of the glacial refuge in the British Isles and their contribution to the post glacial colonization of Scandinavia and the North Atlantic islands. Pp. 407-424 *in* Erwin, T.L., G.E. Ball, D.R. Whitehead, and A.L. Halpern (editors), **Carabid Beetles: Their Evolution, Natural History, and Classification.** Dr. W. Junk Publishers, The Hague. 635 pp.

Cott, H.B. 1940. **Adaptive Coloration in Animals.** Metheun, London. xxxii+508pp.

Crisci, J.V. and T.F. Stuessy. 1980. Determining primitive character states for phylogenetic reconstruction. **Systematic Botany** 5:112-135.

Crotch, G.R. 1867. On the Coleoptera of the Azores. **Proceedings of the Scientific Meetings of the Zoological Society of London** 1867:359-391.

Csiki, E. 1928. Carabidae: Mormolycinae, Harpalinae I. *In* Junk, W. and S. Schenkling (editors), **Coleopterorum Catalogus**, Vol. 2, part 97, pp. 1-226. W. Junk, Berlin.

Dalla Torre, C.W. von. 1877. Synopsis der Insecten Oberösterreichs. **Verein für naturkunde in österreich ob der Enns, Linz, Jahresbericht** 8:15-74.

Daley, P.F. and M.F. Ryan. 1979. Ultrastructure of antennal sensilla of *Nebria brevicollis* (Fab.) (Coleoptera: Carabidae). **International Journal of Insect Morphology**

and Embryology 8:169-181.

Darlington, P.J., Jr. 1959. The *Bembidion* and *Trechus* (Col.: Carabidae) of the Malay Archipeligo. **Pacific Insects** 1(4):331-345.

___________. 1962. Australian carabid beetles X. *Bembidion*. **Brevioria** 162:1-12.

___________. 1970. Modern taxonomy, reality, and usefulness. **Systematic Zoology** 20:341-365.

Dejean, P.F.M.A. 1831. **Species général des Coléoptères de la collection de M. le Comte Dejean.** vol. 5, pp.I-VIII, 1-384. Paris.

Ekis, G. 1977. Classification, phylogeny and zoogeography of the genus *Perilypus* (Coleoptera: Cleridae). **Smithsonian Contributions to Zoology**, number 227, iv+138 pp.

Eldredge, N. and J. Cracraft. 1980. **Phylogenetic Patterns and the Evolutionary Process. Method and Theory in Comparative Biology.** Columbia University Press, New York. viii+349 pp.

Elias, S.A. 1984. Coleoptera from two subarctic localities in Canada with ecological notes and six new distribution records. **The Coleopterists Bulletin** 38(2):142-144.

2

Emden, F.I. van 1942. A key to the genera of larval

Carabidae (Col.). **Transactions of the Royal Entomological Society of London** 92:1-99.

Erwin, T.L. 1972. Two new genera of bembidiine carabid beetles from Australia and South America with notes on their phylogenetic and zoogeographic significance (Coleoptera). **Brevoria**, number 383. 19pp.

___________. 1973. Studies of the subtribe Tachyina (Coleoptera: Carabidae: Bembidiini), Part I: A revision of the Neotropical genus *Xystosomus* Schaum. **Smithsonian Contributions to Zoology**, number 140, 39 pp.

___________. 1974. Studies of the subtribe Tachyina (Coleoptera: Carabidae: Bembidiini) Supplement A: lectotype designations for New World species, two new genera, and notes on generic concepts. **Proceedings of the Entomological Society of Washington** 76:123-155.

___________. 1975. Studies of the subtribe Tachyina (Coleoptera: Carabidae: Bembidiini), Part III: Systematics, Phylogeny, and Zoogeography of the genus *Tachyta* Kirby. **Smithsonian Contributions to Zoology**, number 208, iii+68 pp.

___________. 1982. Small terrestrial ground-beetles of Central America (Carabidae: Bembidiina and Anillina). **Proceedings of the California Academy of Sciences** 42:455-496.

___________. 1984. Studies of the Tribe Bembidiini (Coleoptera: Carabidae): Lectotype designations and species group assignments for *Bembidion* species described by Thomas L. Casey and others. **Pan-Pacific Entomologist** 60(3):165-187.

___________. 1985. The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles. *In* Ball, G.E. (editor), **Taxonomy, Phylogeny, and Zoogeography of Beetles and Ants. A Volume Dedicated to the Memory of Philip Jackson Darlington, Jr. 1904-1983.** Dr. W. Junk Publishers, The Hague, in press.

Erwin, T.L., and D.H. Kavanaugh. 1981. Systematics and zoogeography of *Bembidion* Latreille: I. The *carlhi* and *erasum* groups of western North America (Coleoptera: Carabidae, Bembidiini). **Entomologica Scandinavica** Supplement 15:33-72.

Erwin, T.L., and L.L. Sims. 1984. Carabid beetles of the West Indies (Insecta: Coleoptera): A synopsis of the genera and checklists of tribes of Caraboidea, and of the West Indian species. **Quaestiones Entomologicae** 20:351-466.

Estabrook, G.F., J.G. Strauch, Jr., and K.L. Fiala. 1977. An application of compatibility analysis to the Blackiths' data on orthopteroid insects. **Systematic Zoology** 26:269-276.

Fabricius, J.C. 1775. **Systema Entomologiae.** Lipsiae, 832 pp.

__________. 1792. **Entomologia Systematica. Emendata et aucta. Secundum classes, ordines, genera, species. Adjectis synonimis, locis, observationibus, descriptionibus.** I(1):i-xx,1-330 + 538 pp. Hafniae.

Fall, H.C. 1910. Miscellaneous notes and descriptions of North American Coleoptera. **Transactions of the American Entomological Society** 36:89-197.

__________. 1916. Three new Coleoptera from Washington state. **Bulletin of the Brooklyn Entomological Society** 11: 13-14.

Farris, J.S. 1982. Outgroups and parsimony. **Systematic Zoology** 31:328-334.

__________. 1983. The logical bases of phylogenetic analysis. Pp. 7-36 *in* N. Platnick and V. Funk (editors), **Advances in Cladistics. Volume 2. Proceedings of the Second Meeting of the Willi Hennig Society.** Columbia University Press, New York.

Felsenstein, J. 1978. The number of evolutionary trees. **Systematic Zoology** 27:27-33.

__________. 1981. A likelihood approach to character weighting and what it tells us about parsimony and compatibility. **Biological Journal of the Linnean**

Society 16:183-196.

___________. 1982. Numerical methods for inferring evolutionary trees. **The Quarterly Review of Biology** 57:379-404.

___________. 1983. Parsimony in systematics: biological and statistical issues. **Annual Review of Ecology and Systematics** 14:313-333.

Gardner, J.C.M. 1938. Immature Stages of Indian Coleoptera (23), Carabidae. **Indian Forest Records** 3(8):149-157.

Gebler, F.A. 1833. Notae et addidamenta ad catalogum coleopterorum Sibiriae Occidentalis et confinis tatariae operis C.F. von Ledebours Reise in das Altaigebirge und die soongarisch Kirgisensteppe. **Bulletin de la Société Impériale des Naturalistes de Moscou** 6:262-309.

Germar, E.F. 1824. **Coleopterorum species novae aut minus cognitae, descriptionibus illustratae.** I. pp. I-XXIV, 1-624. J.C. Hendel and sons, Halle.

Gersdorf, E. 1937. Okologische-faunistische Untersuchungen über die Carabiden der mecklenburgischen Landschaft. **Zoologische Jahrbücher, Abteilung für Systematik, Okologie, und Geographier der Tiere** 70:17-86.

Gordon, R.D. 1985. The Coccinellidae (Coleoptera) of America North of Mexico. **Journal of the New York Entomological**

Society 93:1-912.

Goulet, H. 1977. Technique for the study of immature Coleoptera in glycerine. **The Coleopterists Bulletin** 3(4):381-382.

___________. 1983. The genera of Holarctic Elaphrini and species of *Elaphrus* Fabricius (Coleoptera:Carabidae): classification, phylogeny, and zoogeography. **Quaestiones Entomologicae** 19:219-482.

Guse, G.-W. and K. Honomichl 1980. Die digitiform Sensillen auf dem Maxillarpalpus von Coleoptera. II. Feinstruktur bei *Agabus bipustulatus* (L.) und *Hydrobius fuscipes* (L.). **Protoplasma** 103:55-68.

Gyllenhal, L. 1827. **Insecta Svecica. Classis I. Coleoptera sive Eleuterata.** I(IV), Lipsiae, Apud Friedericum Fleischer.

Hatch, M.H. 1950. Studies on the Coleoptera of the Pacific Northwest. II. Carabidae: Bembidiini. **The Pan-Pacific Entomologist** 26:97-106.

___________. 1951. Studies on the Coleoptera of the Pacific Northwest. IV. Carabidae, Dytiscidae, Gyrinidae. **Bulletin of the Brooklyn Entomological Society** 46:113-122.

Hayward, R. 1897. On the species of Bembidium of America North of Mexico. **Transactions of the American**

Entomological Society 24:32-143.

___________. 1901. Synonomical notes on Bembidium and descriptions of new species. **Transactions of the American Entomological Society** 27:156-158.

Hecht, M.K., and Edwards, J.L. 1976. The methodology of phylogenetic inference above the species level. *In* M.K. Hecht, Goody, P.C., and Hecht, B.M., editors, **Major Patterns in Vertebrate Evolution**, pp. 3-51. NATO Advanced Study Institutes Series. Plenum Press, New York.

Hennig, W. 1966. **Phylogenetic Systematics**. University of Illinois Press, Urbana.

Hlavac, T.F. 1971. Differentiation of the carabid antennal cleaner. **Psyche** 78:51-66.

Honomichl, K. 1980. Die digitiform Sensillen auf dem Maxillarpalpus von Coleoptera. I. Vergleichend-topographische Untersuchung des kutikulären Apparates. **Zoologischer Anzeiger** 204:1-12.

Honomichl, K. and G.-W. Guse 1981. Digitiform sensilla on the maxillar palp of Coleoptera. III. Fine structure in *Tenebrio molitor* L. and *Dermestes maculatus* De Geer). **Acta Zoologica** 62:17-25.

Horn, W. and I. Kahle. 1937. Uber entomologische Sammlungen Entomologen und Entomo-Museologie. **Entomologische**

Beihefte 2-5:vi+536pp.

Howden, A.T. 1976. *Pandeleteius* of Venezuela and Colombia (Curculionidae: Brachyderinae: Tanymecini). **Memoirs of the American Entomological Institute** 24:1-310.

Hůrka, K. 1978. Bestimmunstabellen für die Gattungen ausgewählte Käferfamilien 5.2. Carabidae. Pp. 51-69 *in* B. Klausnitzer, (editor), **Ordnung Coleoptera (Larven).** Dr. W. Junk, The Hague, 378 pp.

Jeanne, C. 1971. Carabiques de la Péninsule Ibérique (12e note). **Bulletin de la Société Linnéenne de Bordeaux** 1:203-220.

Jeannel, R. 1941. Coléoptères Carabiques, Première Partie. **Faune de France**, 39. Paris, Lechevalier, 571 pp.

___________. 1962. Les Trechides de la Paléantarctide occidentale. **Biologique de Amerique Australe** 1:527-655, 252 figs.

Jedlička, A. 1961. Drei neue Bembidion-Arten aus Japan (Coleoptera, Carabidae). **Annales Historico-Naturales Musei Nationalis Hungarici (Pars Zoologica)** 53:311-???

___________. 1965a. Monographie des Tribus Bembidiini aus Ostasien (Coleoptera, Carabidae). **Entomologische Abhandlungen** 32(7):79-199.

___________. 1965b. Neue Carabiden aus den Samml. des

Riksmuseum in Stockholm. **Entomologisk Tidskrift** 86:202-208.

Jong, R. de. 1980. Some tools for evolutionary and phylogenetic studies. **Zeitschrift für zoologische Systematik und Evolutionsforschung** 18:1-23.

Juberthie, C. and Z. Massoud. 1977. L'équipment sensoriel de l'antenne d'un coléoptère troglobie, *Aphaenops cryticola* Linder (Coleoptera: Trechinae). **International Journal of Insect Morphology and Embryology** 6:147-160.

Kavanaugh, D.H. 1978. The Nearctic species of *Nebria* Latreille (Coleoptera: Carabidae: Nebriini): classification, phylogeny, zoogeography, and natural history. Unpublished PhD thesis. University of Alberta, Edmonton.

____________. 1979. Studies of the Nebriini (Coleoptera: Carabidae), III. New Nearctic *Nebria* species and subspecies, nomenclatural notes, and lectotype designations. **Proceedings of the California Academy of Sciences** 42:87-133.

Keleinikova, S.I. 1976. Motschulsky's types of Coleoptera in the collection of the Zoological Museum MGU. I. Carabidae. [In Russian.] **Sbornik Trudov Gosudarstvennogo Zoologicheskogo Museya** 15:183-224.

Kirby, W. 1837. The Insects. *In*, J. Richardson, **Fauna**

Boreali-Americana; or the zoology of the northern parts of British America. 4:1-325.

Kirk, V.M. 1972. Identification of ground beetle larvae found in cropland in South Dakota. **Annals of the Entomological Society of America** 65:1349-1356.

Kluge, A.G., and J.S. Farris. 1969. Quantitative phyletics and the evolution of anurans. **Systematic Zoology** 18:1-32.

Krynicki, J. 1832. Enumeratio coleopterorum rossiae meridionalis et praecipue in Universitatis Caesareae Charkoviensis circulo obvenientium, quae annorum 1827-1831 spatio observavit. **Bulletin de la Société Impériale Naturalistes de Moscou** 5:65-179.

Kryzhanovskij, O.L. 1976. An attempt at a revised classification of the family Carabidae (Coleoptera). **Entomological Review** 1:56-64.

____________. 1983. Coleoptera. Vol I, no. 2. Adephaga (Part 1). **Fauna of the U.S.S.R.**, new series no. 128, Leningrad. 341 pp.

Kuhnt, P. 1913. **Illustrierte bestimmungs-tabellen der Käfer Deutschlands. Ein handbuch zum genauen und leichten bestimmen aller in Deutschland vorkommenden Käfer.** E. Schweizerbart'sche verlagsbuchhandlung, Nägele and Dr. Sproesser, Stuttgart. 1138 pp.

Lamb, W.K. 1971. **Canada's Five Centuries. From Discovery to Present Day.** McGraw-Hill, Toronto. 327pp.

Landry, J.-F., and Y. Bousquet. 1984. The genus *Omophron* Latreille (Coleoptera: Carabidae): redescription of the larval stage and phylogenetic considerations. **The Canadian Entomologist** 116:1557-1569.

Larochelle, A. 1975. Notes sur l'activité diurne de quelques Carabidae du Québec. **Annales de la Société Entomologique du Québec** 20:3-6.

___________. 1977. *Bembidion* du Québec: group *inaequale*. **Fabreries** 3(3):38-40.

Larsson, S.G. 1939. Entwicklungstypen und Entwicklungszeiten der dänischen Carabiden. **Entomologiske Meddelelser** 20:277-560.

___________. 1941. Larver. In V. Hansen (editor), Biller XI. Sandspringere og løbebiller. **Danmarks Fauna** 47:243-380. [Not seen.]

___________. 1968. Larverne. In V. Hansen (editor), Biller XXIV. Sandspringere og løbebiller (Cicindelidae og Carabidae). **Danmarks Fauna** 76:282-433.

Latreille, P.A. 1802. **Histoire naturelle, générale et particulière des crustaces et des insectes. Familles naturelles des genres**, vol. 3. Paris. 467 pp.

LeConte, J.L. 1848. A descriptive catalogue of the geodephagous Coleoptera inhabiting the United States east of the Rocky Mountains. **Annals of the Lyceum of Natural History of New York** 4:173-233, 334-474.

___________. 1851. Descriptions of new species of Coleoptera, from California. **Annals of the Lyceum of Natural History of New York** 5:125-216.

___________. 1878. The Coleoptera of the alpine regions of the Rocky Mountains. **Bulletin of the United States Geological and Geographical Survey of the Territories** 4(2):447-480.

Lindroth, C.H. 1940. Zur Systematik fennoskandischer Carabiden. 4-12. Bembidion-Studien. **Notulae Entomologicae** 19:63-99.

___________. 1945, 1949. Die fennoskandischen Carabidae. I. **Göteborgs Kungliga Vetenskap och Vitterhets-Samhälles Handlingar** Ser. B4. I: 709 pp., II: 277 pp., III: 911 pp.

___________. 1954. Random notes on North American Carabidae (Coleopt.). **Bulletin of the Museum of Comparative Zoology** 111(3):117-161.

___________. 1955. The carabid beetles of Newfoundland, including the French islands St. Pierre and Miquelon. **Opuscula Entomologica Supplementum** XII, 168pp.

___________. 1957a. The Linnean species of carabid beetles. **Journal of the Linnean Society - Zoology** 43: 325-341.

___________. 1957b. The principal terms used for male and female genitalia in Coleoptera. **Opuscula Entomologica** 22:241-256.

___________. 1962. Revision of the subgenus *Chrysobracteon* Net., genus *Bembidion* Latr. (Col. Carabidae). **Opuscula Entomologica** 27:1-18.

___________. 1963. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Part 3. **Opuscula Entomologica**, Supplementum XXIV, pp. 201-408.

___________. 1965. Two new species of subg. *Chrysobracteon* (genus *Bembidion*), from Alaska and Siberia (Col. Carabidae). **Opuscula Entomologica** 30:125-128.

___________. 1969. The ground-beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Part 6. **Opuscula Entomologica** Supplementum XXXIV, pp. 945-1192.

___________. 1974a. Coleoptera, Carabidae. **Handbook for the Identification of British Insects** IV(2):1-148.

___________. 1974b. On the elytral microsculpture of carabid beetles (Col. Carabidae). **Entomologica Scandinavica** 5:251-264.

___________. 1975. Designation of holotypes and lectotypes among ground beetles (Coleoptera, Carabidae) described by Thomas L. Casey. **The Coleopterists Bulletin** 29(2):109-147.

____________. 1976. Genus *Bembidion* Latreille (Coleoptera: Carabidae) in New Zealand: a revision. **New Zealand Journal of Zoology** 3:161-198.

____________. 1980. A revisionary study of the taxon *Cillenus* Samouelle, 1819 and related forms (Coleoptera: Carabidae, Bembidiini). **Entomologica Scandinavica** 11:179-205.

Lindroth, C.H. and R. Freitag. 1969. North American ground-beetles (Coleoptera, Carabidae, excluding Cicindelinae) described by Thomas Say: designation of lectotypes and neotypes. **Psyche** 76:326-361.

Linné, C. von. 1761. **Fauna Suecica. Sistens Animalia Sueciæ Regni: Mammalia, Aves, Amphibia, Pisces, Insecta, Vermes. Distributa per classes & ordines, genera & species, cum differentiis specierum, synonymis auctorum, nominibus incolarum, locis natalium, descriptionibus insectorum.** Second edition. 578 pp. Laurent Salv, Stockholm.

Maddison, D.R. 1985. Chromosomal diversity and evolution in the ground beetle genus *Bembidion* and related taxa (Coleoptera: Carabidae: Trechitae). **Genetica** 66:93-114.

___________. MS. Meiotic systems of caraboid beetles, with special reference to male achiasmate meiosis in *Bembidion*. (Coleoptera: Carabidae and Trachypachidae).

Maddison, W.P., M.J. Donoghue, and D.R. Maddison. 1984. Outgroup analysis and parsimony. **Systematic Zoology** 33:83-103.

Matthews, J.V., Jr. 1976. Insect fossils from the Beaufort Formation: geological and biological significance. **Geological Survey of Canada** Paper 76-1B:217-227.

___________. 1977. Tertiary Coleoptera fossils from the North American arctic. **The Coleopterists Bulletin** 31(4):297-308.

___________. 1979. Late Tertiary carabid fossils from Alaska and the Canadian Archipelago. Pp. 425-445 *in* Erwin, T.L. G.E. Ball, D.R. Whitehead, and A.L. Halpern (editors), **Carabid Beetles: Their Evolution, Natural History, and Classification**. Dr. W. Junk Publishers, The Hague, 635 pp.

Meier, W. 1899. Über Abänderungen einiger Coleopteren-Arten, welche bei Hamburg gefunden wurden. **Entomologische Nachrichten** 25:97-102.

Moore, B.P. 1979. Chemical defense in carabids and its bearing on phylogeny. Pp. 193-203 in Erwin, T.L., G.E. Ball, D.R. Whitehead, and A.L. Halpern (editors),

Carabid Beetles: Their Evolution, Natural History, and Classification Dr. W Junk Publishers, The Hague, 635 pp.

Morawitz, A. 1862. Vorläufige Diagnosen neuer Coleopteren aus Südost-Sibirien. **Bull. Acad. Imp. Sci., Leningrad** 5:231-265. [Not seen.]

Mörch, O.A.L. 1853. Catalogus Conchyliorum Yoldi. 2:18. [Not seen.]

Motschulsky, V. von. 1845. Insectes de la Sibérie rapportés d'un voyage fait en 1839 et 1840. **Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg** 13:1-274.

___________. 1850. **Die Kæfer Russlands.** I. Insecta Carabica. vii+91 pp.+9 tables. Gautier, Moscow.

___________. 1859. Coléoptères nouveaux de la Californie. **Bulletin de la Société Impériale des Naturalistes de Moscou** 32(2):122-185.

Müller, J. 1918. Bestimmungstabelle der *Bembidion*-Arten Europas und des Mittelmeergebietes. **Koleopterologische Rundschau** 7:26-117. [Not seen.]

___________. 1926-1927. Tableaux de détermination des coléoptères d'Europe. Heft LXXXIX (89). Carabidae. Genre *Bembidium* Latr. d'Europe et de la région méditerranéenne. **Miscellanea Entomologica** 29-30:1-100.

[French translation of Müller (1918).]

Négre, J. 1973. The zoological results of Gy. Topál's collectings in south Argentine 24. Coléoptères: Carabidae. **Folia Entomologica Hungarica. Rovartani Közlemények** (new series), 26:289-310.

Nelson, G. 1978. Ontogeny, phylogeny, paleontology, and the Biogenetic Law. **Systematic Zoology** 27:324-345.

___________. 1983. Reticulation in cladograms. Pp. 105-111 *in* N. Platnick and V. Funk (editors), **Advances in Cladistics. Volume 2. Proceedings of the Second Meeting of the Willi Hennig Society**. Columbia University Press, New York.

Netolitzky, F. 1910. Bemerkungen zur Systematik in der Gattung Bembidion Latr. **Wiener Entomologische Zeitung** 29:209-228.

___________. 1914a. Die Bembidiini in Winklers Catalogus. I-II. **Entomologische Blätter** 10:50-55, 164-176.

___________. 1914b. *Bembidion (Bracteon) fusiforme* nov. spec. (Col.). **Entomologische Mitteilungen** 3:168-169.

___________. 1921. Catalogus systematicus specierum palaearcticarum generis Bembidion Latr. (Carabidae). **Archiv für Naturgeschichte** Series A, 87(7):185-229.

___________. 1926. Bemerkungen über Bembidion-Larven.

Entomologische Blätter 22:117-119.

____________. 1927. Gedanken über die Urform und das natürlische System der *Bembidiini* und der mit ihnen nächstverwandten Carabidengruppen. **Koleopterologische Rundschau** 13:100-112.

____________. 1928. *Bembidion Gebieni* n. sp. aus China. **Koleopterologische Rundschau** 14:168.

____________. 1931. Kritisches zum Katalog der Harpalinae von Csiki, etc. **Deutsche entomologische Zeitschrift** 153-167.

____________. 1940. Bestimmungstabellen der Bembidion-Arten Europas, Asiens und Afrikas. **Buletinul Facultătii de Stiinte din Cernăuti.** 13(1939):144-179. [Not seen.]

____________. 1942, 1943. Bestimmungstabellen der *Bembidion*-Arten des paläarktischen Gebietes. **Koleopterologische Rundschau** 28:29-124, 29:1-70.

Netolitzky, F., and P. Meyer. 1933. Die Verbreitung von Bembidion argenteolum. **Entomologische Blätter** vol. 29, 2 unnumbered pages plus 1 map issued with Heft 4.

____________. 1939. Die Verbreitung des *Bembidion velox* L. (Besonders dem Norden und Osten eigen). **Entomologische Blätter** vol. 35, 4 unnumbered pages plus 1 map issued with Heft 4.

Notman, H. 1929. A new species of Bembidion from Lake Superior (Coleoptera, Carabidae). **Journal of the New York Entomological Society** 37:157-158.

Olivier, A.G. 1790. Entomologie, ou histoire naturelle des insectes, avec leurs caractères génériques et spécifiques, leur description, leur synonymie et leur figure eluminée. Coléoptères. vol. 2. 485 pp. Paris.

Orth, D.J. 1967. Dictionary of Alaska Place Names. **Geological Survey Professional Paper 567**. U.S. Government Printing Office, Washington. 1084pp + 12 maps.

Panzer, G.W.F. 1794. **Faunae Insectorum Germanicae, initia. Deutschlands Insecten**. vol. 20:4. Nürnberg, Felsecker.

____________. 1797. **Faunae Insectorum Germanicae, initia. Deutschlands Insecten**. vol. 40:8. Nürnberg, Felsecker.

Patterson, C. 1982. Morphological characters and homology. Pp. 21-74 *in* K.A. Joysey and A.E. Friday, editors, **Problems of phylogenetic reconstruction**. Systematics Association Special Volume 21. Academic Press, London.

Pawlowski, J. 1974. Biegaczowate—Carabidae podrodziny Bembidiinae, Trechinae. **Klucze do oznaczania owadów Polski**, No. 82, 19(3b):1-94. [Not seen.]

Paykull, G. 1798. **Fauna Suecica. Insecta**. I. 358 pp. Joh. F. Edman, Uppsala.

Perrault, G.G. 1981. Etudes sur la tribu des Bembidiini (Coleoptera, Carabidae) I. Notes sur la classification supraspécifique. **Nouvelle Revue d'Entomologie** 11:237-250.

____________. 1982. Etudes sur la tribu des Bembidiini s.str. (Coleoptera, Carabidae). II. Révision du sous-genre Cyclolopha (Casey). **Entomologica Basiliensia** 7:89-126.

Perris, E. 1862. Histoire des insects du pin maritime. Suppément aus coléoptères et rectifications. **Annales de la Société Entomologique de France** Ser. 4, 2:173-243, pl. 5-6.

Platnick, N.I. 1979. Philosophy and transformation of cladistics. **Systematic Zoology** 28:537-546.

Raynaud, P. 1976a. Description de deux larves de Coléoptères Carabiques. **Entomops** 38:195-198.

____________. 1976b. Description de cinq larves de Coléoptères Carabiques. **Entomops** 40:275-284.

____________. 1977. Description de deux larves de Coléoptères Carabiques. **Entomops** 41:8-12.

Reed, E.C. 1874. On the Coleoptera Geodephaga of Chile. **Proceedings of the Zoological Society (London)** 1874:48-70, plate XIII.

Reichardt, H. 1977. A synopsis of the genera of neotropical

Carabidae (Insecta: Coleoptera). **Quaestiones Entomologicae** 13:346-493.

Rey, C. 1887. Essài d'études sur certains larves de coléoptères et description de quelques espèces inédites ou peu connues. Beaune, 1887, 126pp., 2 pl. [Not seen.]

Robertson, J.G. 1961. Ovariole numbers in Coleoptera. **Canadian Journal of Zoology** 39:245-263.

Rosen, D.E. 1978. Vicariant patterns and historical explanation in biogeography. **Systematic Zoology** 27:159-188.

____________. 1979. Fishes from the uplands and intermontane basins of Guatemala: Revisionary studies and comparative biogeography. **Bulletin of the American Museum of Natural History** 162:267-376.

Ross, H.H. 1974. **Biological Systematics**. Addison-Wesley, Reading, Massachusetts. 345pp.

Rożek, M. 1981. Karyological studies of *Bembidiinae (Coleoptera, Carabidae)*. I. Chromosome number and sex-determining system in six species of the genus *Bembidion* Latr. **Folia Biologica** (Kraków) 29(2):119-122.

Rye, B.G. 1908. Biller. I. Løbebiller. **Danmarks Fauna.** 178pp.

Sahlberg, J. 1880. Bidrag till Nordvestra Sibiriens

Insektfauna. Coleoptera. Insamlade under expeditionerna till Obi och Jenessej 1876 och 1877. I. Cicindelidæ, Carabidæ, Dytiscidæ, Hydrophilidæ, Gyrinidæ, Dryopidæ, Georyssidæ, Limnichidæ, Heteroceridæ, Staphilinidæ, och Micropeplidæ. **Kongilga Svenska Vetenskaps-akademiens Handlingar** 17(4):1-115 + 1 plate.

Say, T. 1823a. Descriptions of coleopterous insects collected in the late expedition to the Rocky Mountains, performed by order of Mr. Calhoun, Secretary of War, under the command of Major Long. **Journal of the Academy of Natural Sciences** (Philadelphia) 3:139-216.

____________. 1823b. Descriptions of insects of the families of Carabici and Hydrocanthari of Latreille, inhabiting North America. **Transactions of the American Philosophical Society** 2:1-109.

____________. 1834. Descriptions of new North American insects and observations on some already described. **Transactions of the American Philosophical Society**, new series, 4:409-470.

Schaum, H.R. 1859. Drei neue carabicinen-larven. **Berliner entomologische Zeitschrift** 3:35-41, pl. 4, figs.1-3.

Schildknecht, H., U. Maschwitz, and H. Winkler. 1968. Zur evolution der Carabiden-Wehrdrüsensekrete. Uber Arthropoden-Abwehrstoffe XXXII. **Die Naturwissenschaften** 55:112-117.

Schilsky, J. 1908. XII. Beitrag zur deutschen Käferfauna. **Deutsche Entomologische Zeitschrift** pp.604-608.

Schiødte, J.C. 1867. De Metamorphosi Eleutheratorum Observationes. Bidrag til Insekterns Udviklingshistorie. **Naturhistorisk Tiddsskrift** 3(4):415-552.

Schuler, L. 1959. Le genre *Microserrulula* Netolitzky (Bembidiini Jeannel, Col. Trechidae) les formes multispires. **Revue française d'Entomologie** 26:96-105.

___________. 1960. Les spermathèques dans las tribu des Bembidiini Jeannel (Col. Trechidae). **Revue française d'Entomologie** 27:24-48.

___________. 1971. Les Trechinae de France. L'inversion de la valuer systematique des organes genitaux males et femelles. **Novelle Revue d'Entomologie** 1(3):265-274.

Seidlitz, G. 1891. Die Kaefer (Coleoptera) der deutschen ostseeprovinzen Russlands. **Fauna Baltica**, second edition. lvi+192+819 pp. Königsberg.

Serrano, J. 1981a. Chromosome numbers and karyotypic evolution of Caraboidea. **Genetica** 55:51-60.

Serrano, J. 1981b. A chromosome study of Spanish Bembidiidae and other Caraboidea (Coleoptera, Adephaga). **Genetica** 57:119-129.

Serrano, J. 1981c. Male achiasmatic meiosis in Caraboidea. **Genetica** 57:131-137.

Serrano, J. 1984. New chromosome numbers of Spanish Caraboidea (Coleoptera, Adephaga). **Genética Ibérica** 34(1982):63-82.

Serville, J.G.A. 1826. **Faune Française, Insectes. Coléoptères.** 240pp. [Not seen.]

Sharova, I.K. 1958. The larvae of Carabidae beneficial and noxious to agriculture. **Uchenye Zapiski Moskovskogo Gosudarstvennogo Pedagogicheskogo Instituta Imeni Lenina** 124:1-165. [In Russian; not seen.]

Sharp, D. 1903. Coleoptera Caraboidea. **Fauna Hawaiiensis,** 3:175-292. [Not seen.]

Silvey, J.K.G. 1935. An investigation of the burrowing inner-beach insects of some fresh-water lakes. **Papers from the Michigan Academy of Arts, Science and Letters** 21:655-697.

Simberloff, D., Heck, K.L., McCoy, E.D., and E.F. Connor. 1981. There have been no statistical tests of cladistic biogeographic hypotheses. Pp. 40-63 *in* Nelson, G., and D.E. Rosen (editors), **Vicariance Biogeography: a Critique.** Columbia University Press, New York, xvi+593 pp.

Simpson, G.G. 1961. **Principles of Animal Taxonomy**. Columbia University Press, New York. xii+247 pp.

Smith, S.G. 1960. Chromosome numbers of Coleoptera. II. **Canadian Journal of Genetics and Cytology** 2:66-88.

Smrž, J. 1979. Uber die Larven der *Bembidion* (*Peryphus*)-Arten (Coleoptera, Carabidae, Bembidiinae). **Acta entomologica bohemoslovaca** 76:244-254.

Sober, E. 1983a. Parsimony in systematics: philosophical issues. **Annual Review of Ecology and Systematics** 14:335-357.

___________. 1983b. Parsimony methods in systematics. Pp. 37-48 *in* N. Platnick and V. Funk (editors), **Advances in Cladistics. Volume 2. Proceedings of the Second Meeting of the Willi Hennig Society**. Columbia University Press, New York.

Spence, J.R., and Sutcliffe, J.F. 1982. Structure and function of feeding in larvae of *Nebria* (Coleoptera: Carabidae). **Canadian Journal of Zoology** 60:2382-2394.

Stebbing, E.P. 1914. **Indian Forest Insects of Economic Importance. Coleoptera**. London, Eyre & Spottiswoode, Ltd. xvi + 648 pp.

Stevens, P.F. 1980. Evolutionary polarity of character states. **Annual Review of Ecology and Systematics** 11:333-358.

Stork, N.E. 1980. A scanning electron microscope study of tarsal adhesive setae in the Coleoptera. **Zoological Journal of the Linnean Society** 68:173-306.

Sturm, J. 1825. **Deutschlands Fauna in Abbildungen nach der Natur mit Beschreibungen. V. Abtheilungen Die Insecten.** vol. 6, 188pp.

____________. 1843. **Catalog der Kæfer-Sammlung.** J. Sturm, Nürenberg. 386 pp.

Thompson, R.G. 1979. Larvae of North American Carabidae with a key to the tribes. Pp. 209-291 *in* Erwin, T.L., G.E. Ball, D.R. Whitehead, and A.L. Halpern, editors, **Carabid Beetles: Their Evolution, Natural History, and Classification.** Dr W. Junk Publishers, The Hague, 635 pp.

Turin, H., J. Haeck, and R. Hengeveld. 1977. **Atlas of the carabid beetles of The Netherlands.** North-Holland Publishing Company, Amsterdam.

Uéno, S.-I. 1955. Marine insects of the Tokara Islands. VII. New species and new subspecies of the subfamily Trechinae (Coleoptera, Harpalidae). **Publications of the Seto Marine Biological Laboratory** 4:403-413.

Uyttenboogaart, D.L. 1904. in Everts, Tweede Lijst van soorten en varieteiten nieuw voor de Nederlandsche fauna, sedert de uitgave der "Coleoptera Neerlandica" bekend geworden. **Tijdschrift voor Entomologie** 47:172-176.

Voorzanger, B., and W.J. van der Steen. 1982. New perspectives on the Biogenetic Law? **Systematic Zoology** 31:202-205.

Wagner, H. 1915. Beiträge zur Coleopterenfauna der Mark Brandenburg II. **Entomologische Mittleilungen** 4:300-309.

Wanntorp, H.-E. 1983. Reticulated cladograms and the identification of hybrid taxa. Pp. 81-88 *in* N. Platnick and V. Funk (editors), **Advances in Cladistics. Volume 2. Proceedings of the Second Meeting of the Willi Hennig Society**. Columbia University Press, New York.

Watrous, L.E. and Q.D. Wheeler. 1981. The out-group comparison method of character analysis. **Systematic Zoology** 30:1-11.

Whitehead, D.R. 1972. Classification, phylogeny, and zoogeography of *Schizogenius* Putzeys (Coleoptera: Carabidae: Scaritini). **Quaestiones entomologicae** 8:131-348.

Wiley, E.O. 1978. The evolutionary species concept reconsidered. **Systematic Zoology** 27:17-26.

____________. 1981. **Phylogenetics. The Theory and Practice of Phylogenetic Systematics**. John Wiley and Sons, New York. xv+439pp.

Wollaston, T.V. 1877. Coleoptera Sanctæ-Helenæ. 8vo., 256pp. [Not seen.]

Xambeau, V. 1894. Moeurs et métamorphoses d'insectes. 5e mémoire. **Annales de la Sociétié Linnéenne de Lyon** 41:107-156.

Zacharuk, R.Y., P.J. Albert, and F.W. Bellamy. 1977. Ultrastructure and function of digitiform sensilla on the labial palp of a larval elaterid (Coleoptera). **Canadian Journal of Zoology** 55:569-578.

Zetterstedt, J.W. 1828. **Fauna Insectorum Lapponica**, Part I. xx+563 pp. Librariea Schulziana, Hammone.

Appendix: numbers of specimens of *Chrysobracteon* studied

Table 9. Number of specimens examined for each data entry of Table 2.
Species abbreviations: **bl**: *B. balli*, **fo**: *B. foveum*, **ar**: *B. argenteolum*, **al**: *B. alaskense*, **sm**: *B. semenovi*, **st**: *B. stenoderum*, **ca**: *B. carinula*, **vx**: *B. velox*, **lp**: *B. lapponicum*, **pn**: *B. punctatostriatum*, **hs**: *B. hesperium*, **lq**: *B. lorquinii*, **ze**: *B. zephyrum*, **lvl**: *B. levettei levettei*, **lvc**: *B. levettei carrianum*, **in**: *B. inaequale*, **lt**: *B. litorale*, **bk**: *B. baikaloussuricum*.

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	bk
1. mirrors on interval 3	150	300	100	100	1	20	500	50	200	200	100	100	500	100	500	700	100	20
2. mirrors on intervals 4 or 5	150	300	100	100	1	20	500	50	200	200	100	100	500	100	500	700	100	20
3. mirrors on intervals 6 or 7	20	20	20	20	1	20	50	20	20	20	20	20	100	50	100	100	50	20
4. interval 7 mirror isolated?	.	.	.	.	1	20	.	.	20	.	20	.	100	50	100	100	50	20
5. silver spot on interval 4?	10	10	10	10	1	10	10	10	10	10	10	10	10	10	10	10	10	10
6. elytral sculpticell shape	6	6	6	6	1	15	6	6	6	6	6	6	6	6	6	6	6	6
7. suborbital setae	6	7	7	7	1	7	7	7	7	7	7	7	7	7	7	7	7	7
8. midlateral pronotal setae	150	300	100	100	1	20	500	50	200	200	100	100	500	100	500	700	100	20
9. ed3 and ed5 - position relative to interneur 3	10	10	10	10	1	10	10	10	10	10	10	10	10	10	10	10	10	10
10. ed3 and ed5 - position relative to silver spot	20	10	20	10	1	10	10	10	10	15	10	10	10	10	10	10	10	10
11. # setae between eo4 & eo5	20	20	20	20	1	12	20	11	11	14	10	14	15	15	15	30	13	7
12. # setae ed7 area	12	12	12	12	1	12	12	12	12	12	12	12	12	12	12	20	12	12
13. male adhesive setae	5	5	2	2	1	2	2	2	2	2	2	2	2	2	2	4	2	2
14. protarsomere 4 ventroapical setae	5	5	5	7	1	6	6	4	5	5	5	6	4	3	2	2	3	2
15. protarsomere 4 setal separation	6	6	10	7	1	6	6	4	7	8	7	6	6	7	7	11	7	2
16. mandible shape	6	6	6	6	1	6	6	6	6	6	6	6	6	6	6	12	6	6
17. lacinia shape	6	6	6	6	1	6	6	6	6	6	6	6	6	6	6	12	6	6
18. lacinia width	6	6	6	6	1	6	6	6	6	6	6	6	6	6	6	12	6	6
19. mentum tooth shape	6	9	6	8	1	7	8	10	10	12	8	8	8	8	10	20	7	3
20. mentum tooth emarginate?	6	9	6	8	1	7	8	10	10	12	8	8	8	8	10	20	7	3
21. mentum tooth bulbous?	6	9	6	8	1	7	8	10	10	12	8	8	8	8	10	20	7	3
22. mentum epilobes	6	9	6	8	1	7	8	10	10	12	8	8	8	8	10	20	7	3
23. pronotal shape	150	300	100	100	1	20	500	50	200	200	100	100	500	100	500	700	100	20
24. pronotal carina	16	20	20	20	1	20	70	30	40	20	20	20	20	20	20	20	20	20
25. metasternum	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	4	2	2
26. elytral basal impression	12	20	12	12	1	12	25	12	12	12	12	12	12	12	12	12	12	12
27. angulate humeral margin	20	20	8	8	1	8	8	8	8	8	8	8	8	8	8	8	8	8
28. interneur 4 shape	150	300	100	100	1	20	500	50	200	200	100	100	500	100	500	700	100	20
29. elytra around ed3 and ed5 foveolate?	150	300	100	100	1	20	500	50	200	200	100	100	500	100	500	700	100	20
30. elytral punctures	6	6	6	6	1	6	6	6	6	6	6	6	6	6	6	6	6	6
31. interneur 8 depth	6	6	6	6	1	6	6	6	6	6	6	6	6	6	6	6	6	6
32. interval 5 posteriorly	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	4	2	2

Table 9, *cont'd.*

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	bk
33. subapical elytral plica	2	2	2	2	1	2	2	2	2	2	2	2	2	2	2	4	2	2
34. male protarsomere 3 shape	5	4	10	7	1	5	4	5	7	5	6	5	6	3	3	6	4	3
35. protarsomere 4 projection	7	7	6	4	1	7	5	4	6	6	6	6	5	6	8	11	6	4
36. flagellar sheath	3	3	3	3	1	3	3	3	3	3	3	3	3	3	3	3	3	3
37. CSC right lobe	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
38. CSC right lobe ridge	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
39. VSP dorsal ridge	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
40. VSP dorsal ridge sculpture	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
41. dark spot on flagellar sheath	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
42. ostial microtrichial patch size	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
43. ostial microtrichia	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
44. ostial sclerotized strip	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
45. pillow with scales	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
46. internal sac leftmost central membrane	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
47. ventral bulge	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
48. aedeagal apex	31	72	20	18	1	9	43	19	56	24	29	37	21	46	66	70	24	6
49. vaginal sclerotized plate	5	6	7	5	.	3	5	5	5	5	5	5	5	5	5	9	3	2
50. spermatheca apically indented?	3	3	3	3	.	3	3	3	3	3	3	3	3	3	3	3	3	3
51. stylomere 1 setal length	5	6	7	5	.	3	5	5	5	5	5	5	5	5	5	9	3	2
52. stylomere 2 length	3	3	4	4	.	3	3	3	3	3	3	3	.	3	5	6	3	2
53. #dorsolateral sensilla	5	6	7	5	.	3	5	5	5	5	5	5	5	5	5	9	3	2
54. sternum X setation	5	6	7	5	.	3	5	5	5	5	5	5	5	5	5	9	3	2
55. autosome number	10	29	.	11	.	.	17	.	30	10	9	7	10	5	38	24	.	.
56. Y chromosome size	4	8	.	5	.	.	7	.	9	4	3	2	3	2	11	8	.	.
57. L$_1$ frontale 3-spotted?	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
58. head (other than spots)	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
59. frontale behind FR$_3$	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
60. frontale - anteriorly behind FR$_3$	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
61. parietal eggbursters	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
62. pronotal microtubercles	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
63. seta FR$_1$ width	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
64. seta FR$_3$ width	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
65. seta PR$_4$ length	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
66. seta PR$_{10}$ length	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
67. gPR & gME lateral setae	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
68. seta PR$_{11}$ size	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
69. seta ME$_2$ length	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
70. seta ME$_{14}$ length	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.

Table 9, *cont'd.*

Character	bl	fo	ar	al	sm	st	ca	vx	lp	pn	hs	lq	ze	lvl	lvc	in	lt	bk
71. seta TE_8 length	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
72. seta TE_{11} length	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
73. seta TE_{11} shape	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
74. seta $TE\alpha$ (near TE_8)	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
75. seta EP_1 length	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
76. segment VIII seta EP_1 width	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
77. seta ST_2 on segment IX	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
78. mandible mesal margin	4	4	.	6	.	.	6	.	5	8	8	7	5	4	7	9	.	.
79. L_2 extra setae near FR_1	2	.	.	3	.	.	2	.	1	1	2	1	1	1	2	2	.	.
80. L_2 stipites	2	.	.	3	.	.	2	.	1	1	2	1	1	1	2	2	.	.
81. L_2 # urogomphus setae	2	.	.	3	.	.	2	.	1	1	2	1	1	1	2	2	.	.

VITA

I was born in London, Ontario, on 27 January 1958, to Louise Juana Maddison (*née* Devillez) and Robert John Maddison. Nine minutes later, just three minutes before the stroke of midnight, my twin brother Wayne Paul Maddison was born. He is my only sibling.

I spent my early years in London, and attended for a year and a half Empress Public School. In February of 1965 my family and I moved to Edmonton, where I spent the next six years. It was during this time that Wayne's and my biological interests sprouted. The acquisition of several Golden Nature Field Guides, including the volumes "Insects" and "Butterflies and Moths", helped direct me. Perhaps more important, however, was the constant interest and encouragement my parents displayed toward my meanderings. While in Edmonton I attended both Forest Heights Public School and Hardisty Junior High School.

In spring of 1971 our family returned to Ontario, to settle in Burlington, where my parents still live. Upon arriving in Ontario, we spent time in a motel in Burlington on the shore of Lake Ontario. One day during this soujourn Wayne discovered, on a pile of grass clippings floating in the lake, a female jumping spider belonging to *Phidippus audax*. This find was probably one of the most significant in our young careers, as it sparked an interest in salticids that developed into the main focus of Wayne's present research and a background interest that led to my enthusiasm for beetle systematics. While in Burlington, I attended Nelson High School, where the many good teachers encouraged me in my artistic, biological, and mathematic endeavours. In 1973, our family vacationed by travelling by car to Edmonton. On this trip, Wayne and I collected jumping spiders extensively. These little animals, were, however, mainly under Wayne's care, and, in order that I might have some work just of my own, I began collecting weevils. I collected weevils throughout the trip, but on the north shore of Lake Superior I discovered a *Cicindela limbalis*. This find and a previously collected *C. sexguttata* soon led to a fascination with tiger beetles, and I left weevils far behind. I didn't study other carabids until a few months later, when my discovery of some obviously undescribed tiger beetles (which I named in my notes "*Microcicindela punctulata*") suddenly made me aware of the rest of the carabids; those "*Microcicindela*" were indeed no more (nor less) than *Elaphrus californicus*. At that point I was hooked on carabids, although it wasn't until receiving a marvelously long and inspiring letter from George Ball written on 23 December 1974 that I connected with other students of ground beetles.

Many other events in my life were important to my biological studies, but one of the most significant was surely my attending the International Congress of Entomology in Washington in 1976. Here I met many of the active carabidologists, including Carl Lindroth and Philip

Darlington. This was a great inspiration to me. It was also during this year that I began my entomological illustrations, a hobby that has occupied my time now and again ever since.

From 1976 to 1980 I attended the University of Toronto, from which I received a Bachelor of Science degree, with specialization in Zoology, in 1980. In Toronto, three biologists influenced me greatly: Chris Plowright, James Thomson, and, especially, Klaus Rothfels. Professor Rothfels's honesty in science has been an inspiration to me ever since.

In January of 1981 I arrived in Edmonton, and have remained here since, officially beginning my Master's degree program in September 1981.